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BRITISH MUSEUM NATURAL HISTORY
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BULLETIN OF
THE BRITISH MUSEUM
(NATURAL HISTORY)

GEOLOGY
VOL. 1
1949-1952

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM LONDON : 1949-1952

DATES OF PUBLICATION OF THE PARTS.

No. 1.	12 December	1949
No. 2.	12 December	1949
No. 3.	30 January	1950
No. 4.	31 August	1950
No. 5.	3 August	1951
No. 6.	3 August	1951
No. 7.	28 July	1952
No. 8.	15 May	1952
No. 9.	13 September	1952
No. 10.	16 October	1952

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BRITISH MUSEUM NATURAL HISTORY
13 DEC 1949

THE PTEROBRANCH *RHABDOPLEURA* IN THE ENGLISH EOCENE

H. DIGHTON THOMAS
AND
A. G. DAVIS

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THE PTEROBRANCH *RHABDOPLEURA* IN THE ENGLISH EOCENE

BY
HENRY DIGHTON THOMAS
AND
ARTHUR GEORGE DAVIS

WITH AN APPENDIX ON

THE LONDON CLAY AT LOWER SWANWICK HAMPSHIRE

BY ARTHUR WRIGLEY

Pp. 1–24; *Pls.* 1–3; 4 *Text-figures*

BULLETIN OF
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in 1949, is to be issued in five series, corresponding to the Departments of the Museum.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 1, No. 1, of the Geological series.

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued December 1949 *Price Seven shillings and sixpence*

THE PTEROBRANCH *RHABDOPLEURA* IN THE ENGLISH EOCENE

By HENRY DIGHTON THOMAS *and* ARTHUR GEORGE DAVIS

(*With Plates* 1–3)

SYNOPSIS

A species of *Rhabdopleura*, the first pterobranch to be found fossil, is described from the London Clay of Hampshire. It helps to bridge the gap between the modern representatives of the group and the last dendroid graptolites in the Carboniferous, for which there is strong evidence that they were at least very closely allied to the Pterobranchia.

I. INTRODUCTION

EARLY in 1930 one of us (A. G. D.) brought to the Museum a pebble from the London Clay of Lower Swanwick, Hampshire, on which was a small, encrusting organism. Its identification as a species of *Rhabdopleura*, unknown until then as a fossil, was confirmed by the other author, and it was exhibited as such at a Conversazione of the Staff Association of the Museum on 5 March 1930. For various reasons, including the search at infrequent intervals for additional well-preserved specimens, and, later, the recent war, the description of this remarkable fossil has had to be delayed.

We are indebted to Mr. A. Wrigley for the Appendix on the stratigraphy of the clay-pit at Lower Swanwick; to Dr. Anna B. Hastings and Dr. E. Trewavas for access to Recent material of *Rhabdopleura* in the Museum; to Miss E. C. Humphreys and Mr. J. V. Brown, respectively, for the drawings and photographs illustrating this paper; to the Council of the Palaeontographical Society of London for permission to reproduce Text-fig. 1; and particularly to Dr. Hastings for invaluable discussions on the genus and for her helpful criticisms of the typescript. One of us (A. G. D.) also wishes to acknowledge a Royal Society Government Grant for the field collecting in the course of which the fossils were discovered.

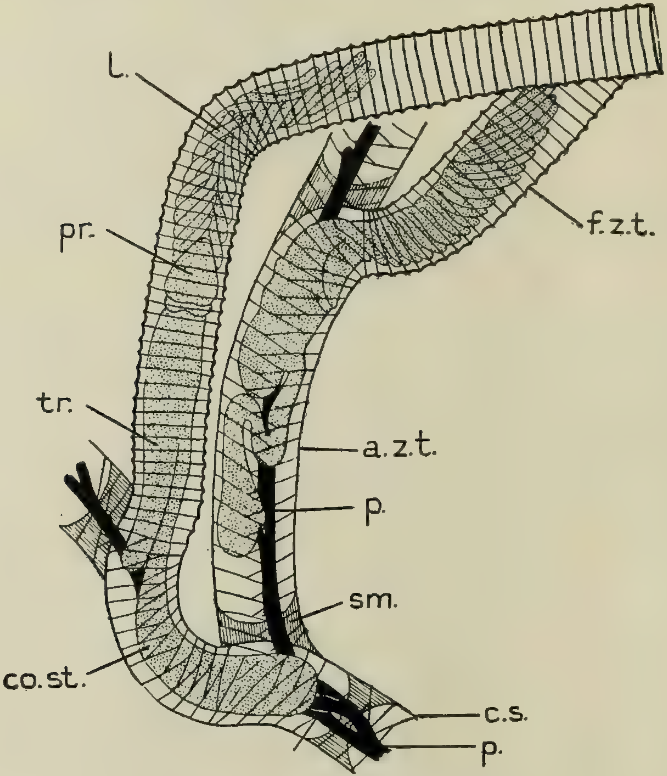
II. THE COENOECIUM OF *RHABDOPLEURA*

(TEXT-FIG. 1)

The following account is mainly based on Lankester (1884), Schepotieff (1907 *a*, *b*), and van der Horst (1936).

Recent species of *Rhabdopleura* are colonial animals which secrete around themselves a series of transparent, chitinous tubes forming the *coenoecium*. The tubes are analogous to those of worm-tubes and do not form an exoskeleton comparable to that, for instance, of the crustacea.

From the point of origin of the colony a bud develops (sometimes there are two developing in divergent directions). The parent bud (immature zooid) moves forwards at the end of a growing soft stalk, *gymnocaulus*, and secretes around itself that part of the tubular coenoecium known as the *creeping stem*, which is cemented by its basal wall to the surface of such underlying foreign bodies as pebbles, corals, ascidians, and shells. The growth-rings of this creeping stem consist of alternating segments which run obliquely backwards from the sides and meet in a zigzag ridge usually along or near the middle of the upper surface—although Norman (1921: 99, fig. 3) shows the zigzag sutures at the sides in *R. annulata* Norman, our observations do not confirm this. The sutures between adjacent bands stand up as oblique ridges. Behind the advancing immature zooid other buds develop from the gymnocaulus to which they remain attached by short branches. Each of these gradually becomes mature, and when it attains a certain size a transverse septum is formed on its distal side across the creeping stem which separates it from the next distal bud, but which is pierced by the gymnocaulus. At a certain stage this young zooid breaks through the wall, usually the upper wall, of the creeping stem and builds its own living tube, the *zooidal tube*, in continuity with it. The zooid remains attached to the original gymnocaulus—the attachment is the *contractile stalk*, by which the zooid can withdraw well within its tube.



TEXT-FIG. 1. *Rhabdopleura normani* Allman.
Two zooidal tubes with retracted, sterile zooids, and part of a creeping stem. ×29.
a.z.t., adherent part of zooidal tube; ***c.s.***, creeping stem; ***co.st.***, contractile stalk; ***f.z.t.***, free part of zooidal tube; ***l.***, lophophore; ***p.***, pectocaulus; ***pr.***, proboscis; ***sm.***, septum; ***tr.***, trunk. (After Bulman, 1945, and Schepotieff, 1907*a*.)

The *zooidal tube* may be upgrowing and not adherent to a foreign body (i.e. free), or it may have a proximal adherent part of a greater or less length in addition to a distal free part. It is because the zooidal tubes are not always wholly free that we introduce that term as preferable to 'free living tubes': there are obvious objections also to 'peristome'. The adherent part of a zooidal tube comes off from the side of the creeping stem and shows similar suturing to it, although, in the fossil species at any rate, the sutures are more closely arranged. The free part, however, is made up of narrow, annular growth-rings: these are separated from one another by prominent circular ridges (sutures), and each is interrupted by an oblique suture marking the junction of its first- and last-formed parts. The terminal immature zooid at the distal end of the gymnocaulus also ultimately becomes mature and forms a vertical, free, zooidal tube—further extension of the creeping stem is then impossible.

The gymnocaulus is free, and it remains so for some distance behind the advancing bud in the creeping stem. But with development it becomes pigmented and chitinized, and forms the *pectocaulus*, the organ which is peculiar to *Rhabdopleura* and which distinguishes it from all other living animals. This term of Lankester's (1884: 635) is better than 'stolon' ('schwarze Stolo' of Schepotieff), for stolons of a different nature are known in other phyla: 'stolon' is best used as a general, descriptive word. The pectocaulus shows as a dark, narrow, cylindrical, rod-like stolon through the transparent chitinous material of the creeping stem. It is composed of an outer and inner cell-layer and is surrounded by a resistant chitinous sheath: its lumen may become filled with a chitinous axial rod. Distally the pectocaulus is free, but with progressive chitinization it first comes to rest against the basal wall of the creeping stem and then becomes adherent to it and finally embedded in it. The proximal end of the contractile stalk of each zooid is also chitinized for a short distance so that short side branches of the pectocaulus exist; indeed, these branches of the pectocaulus may extend along the whole length of the adherent parts of the zooidal tubes (Lankester, 1884: 625, pl. 37 *bis*, figs. 1, 2). Further, the gymnocaulus (and therefore the pectocaulus) may fork, each part giving rise to a series of zooids.

III. *RHABDOPLEURA EOCENICA* Thomas & Davis

PHYLUM CHORDATA

SUB-PHYLUM HEMICHORDA

Class *PTEROBRANCHIA*

Genus RHABDOPLEURA Allman

TYPE SPECIES (by monotypy): *R. normani* Allman, 1869 *a*: 311; 1869 *b*: 439; 1869 *c*: 58, pl. 8. Recent, Shetland seas at 90 fathoms.

Rhabdopleura eocenica Thomas & Davis

PLS. 1–3; TEXT-FIGS. 2–4

1949 *Rhabdopleura eocenica* Thomas & Davis, p. 79

MATERIAL AND HORIZON. Several specimens, mostly fragmentary, preserved in iron pyrites and encrusting flint pebbles at the base of Bed C of the London Clay, Yprésian, Bursledon Brick Company's clay-pit, Lower Swanwick, ⅝-mile ENE. of Bursledon railway station, Hampshire (full National Grid Reference 41/500099)—see Appendix, p. 14.

HOLOTYPE. H.4170a (Pl. 3, fig. 1).

PARATYPES. H.4168–H.4187 (excluding H.4170a) and Geol. Surv. Mus. 83867—most numbers include several specimens.

DIAGNOSIS. *Rhabdopleura* with a creeping stem about 150–195 μ in diameter and growth-rings 60–72 μ wide; zooidal tubes recumbent and adherent proximally but free distally, the adherent parts 150–175 μ in diameter and their growth-rings 40–55 μ wide, the free parts up to 175 μ in diameter and with growth-rings 40–45 μ wide; pectocaulus about 22 μ in diameter.

NOTE ON MEASUREMENTS. Throughout this paper the width of the growth-rings of *R. eocenica*, i.e. the distance apart of the sutures, was measured at *right angles* to the sutures and not in the linear direction of the tubes. That measurement not only gives the true width of the growth-rings, but, in the fossils, is also more accurately made.

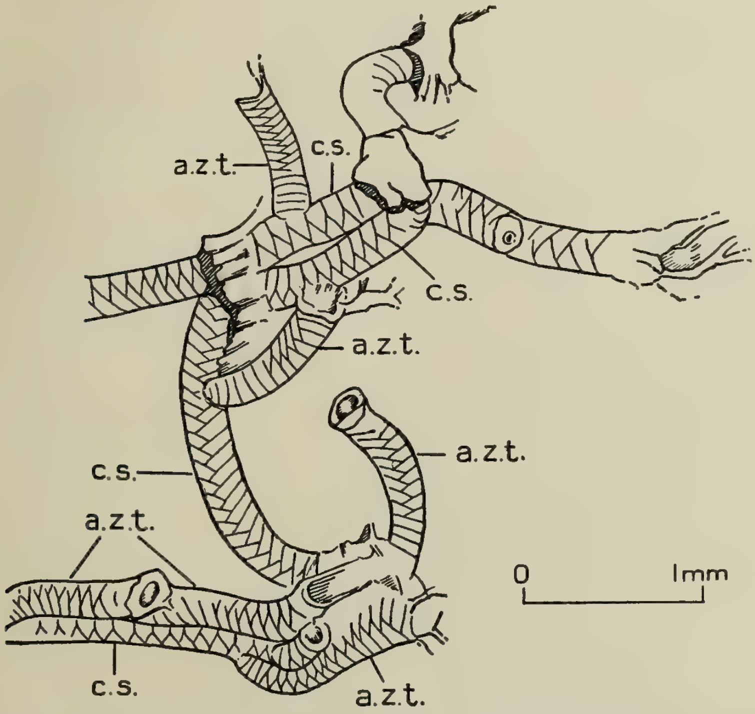
DESCRIPTION:

Coenoecium. The coenoecium is small, the longest piece preserved reaching about 3·5 mm. in length. It is not always possible to follow any one coenoecium far, because the preservation is such that one cannot always be certain whether it has branched or whether it has crossed, or been crossed by, another one. In any case the coenoecia have been broken or worn so that only relatively short lengths are found on the pebbles.

Creeping Stem. The creeping stems are not straight, but may curve extensively. Their basal walls are firmly adherent to the pebbles they encrust. In cross-section these tubes may be approximately semicircular, or they may be sub-triangular, when the sides are flat or nearly so and slope away from the rounded, median upper edge. The sutures are of the type normal in *Rhabdopleura* and meet to give the characteristic median zigzag line on the upper surface. Their distance apart averages between 60 and 72 μ. They are prominent, but the preservation prevents any accurate measurements of the degree to which they project beyond the general width of the tube. Thus the measurements of the width, which varies between 150 and 195 μ, are inclusive of the sutures. Bifurcation of the creeping stems (as distinct from the development of the adherent parts of zooidal tubes) occurs, e.g. in H.4168b and probably in H.4169.

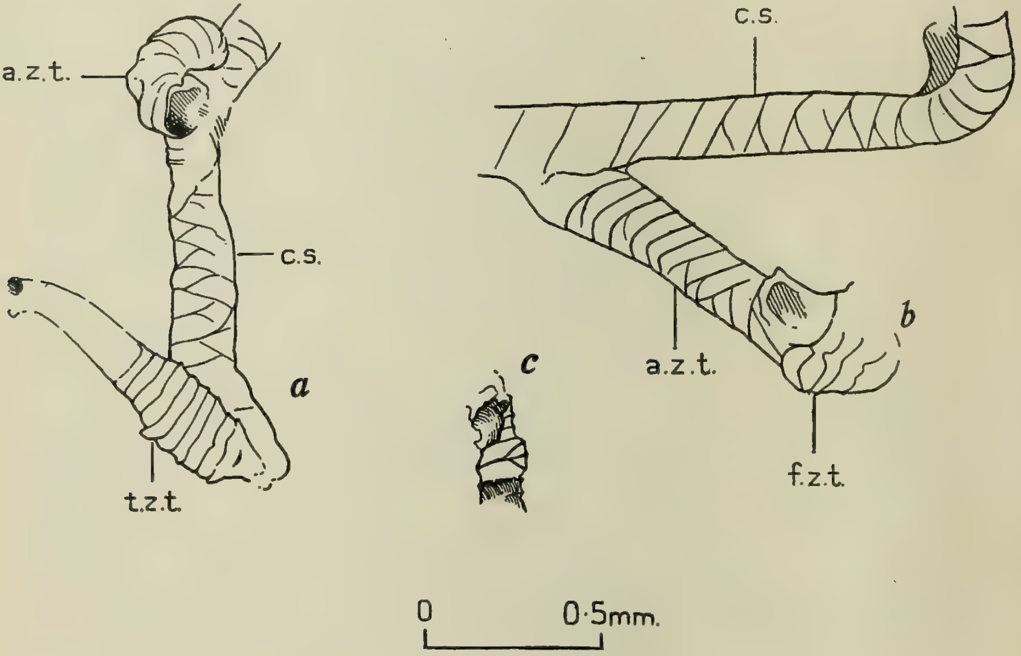
Zooidal Tubes. These develop from the sides of the creeping stems. There is no regularity in their spacing and they are not confined to one side. For example, in H.4169 (Pl. 1; Pl. 2, fig. 1; and Text-fig. 2) four consecutive zooidal tubes come off from a creeping stem at intervals of approximately 630 μ, 412 μ, and 220 μ, respectively, and the later two are developed from the side opposite to that of the first pair.

The zooidal tubes consist of a proximal adherent part and a distal free part. The adherent parts appear usually as relatively short side-branches, between 0·74 and 1·2 mm. long—the length of the complete one which retains part of its free tube (H.4168b) is approximately 0·87 mm. They are generally slightly curved, but they may be much bent and even folded back against themselves. They may lie alongside the creeping stem or at any angle with it up to nearly a right angle, but the initial growth is always partly forwards. They resemble the main creeping stem in appearance because the suturing is similar, but they tend to be more rounded and do not reach the same width (only 150–175 μ), while the sutures are less widely spaced (40–55 μ). The first few sutures (usually three or four), however, where the proximal end swells out of the side of the creeping stem, do not seem to have the alternating, zigzag arrangement, but appear instead to be ring-like (Text-figs. 2, 4). The distal ends of the adherent parts of the tubes are sometimes seen to be slightly turned upwards when they are also somewhat crushed (Pl. 1 and Pl. 2, fig. 1): these are the places where the vertical free parts of the zooidal tubes commenced.



TEXT-FIG. 2. *Rhabdopleura eocenica* Thomas & Davis
A series of intersecting coenoecia, H.4169. (See Pl. 1 and Pl. 2, fig. 1.)
a.z.t., adherent part of zooidal tube; *c.s.*, creeping stem.

The free parts of the zooidal tubes which are preserved are fragments. They include one terminal tube in contact with the creeping stem (H.4168a—Pl. 3, fig. 4, and Text-fig. 3 *a*), several free tubes in contact with their proximal adherent parts (e.g. H. 4170a—Pl. 3, fig. 1; and H.4168b—Pl. 3, fig. 2, and Text-fig. 3 *b*), and some isolated specimens (e.g. H.4171a—Pl. 2, fig. 2). They are generally much flattened and incomplete, and have similar characters. The preserved part of the terminal tube is 500 μ long, but there are indications on the pebble that it was probably at least as long again. The longest free part of a zooidal tube preserved is 3·9 mm. (H.4171a—Pl. 2, fig. 2). The greatest width of a flattened tube is 228 μ, and of a tube which is only slightly crushed 174 μ. The growth-rings are circular and their average width (40–45 μ) is more constant than in the adherent parts of the zooidal tubes.



Text-fig. 3. *Rhabdopleura eocenica* Thomas & Davis

3 *a*. A creeping stem with an adherent part of a zooidal tube and a portion of the terminal zooidal tube (note its probable continuation), H.4168a. (See Pl. 3, fig. 4.)

3 *b*. Specimen retaining the adherent and free parts of a zooidal tube in contact with one another and with the parent creeping stem, H.4168b. (See Pl. 3, fig. 2.)

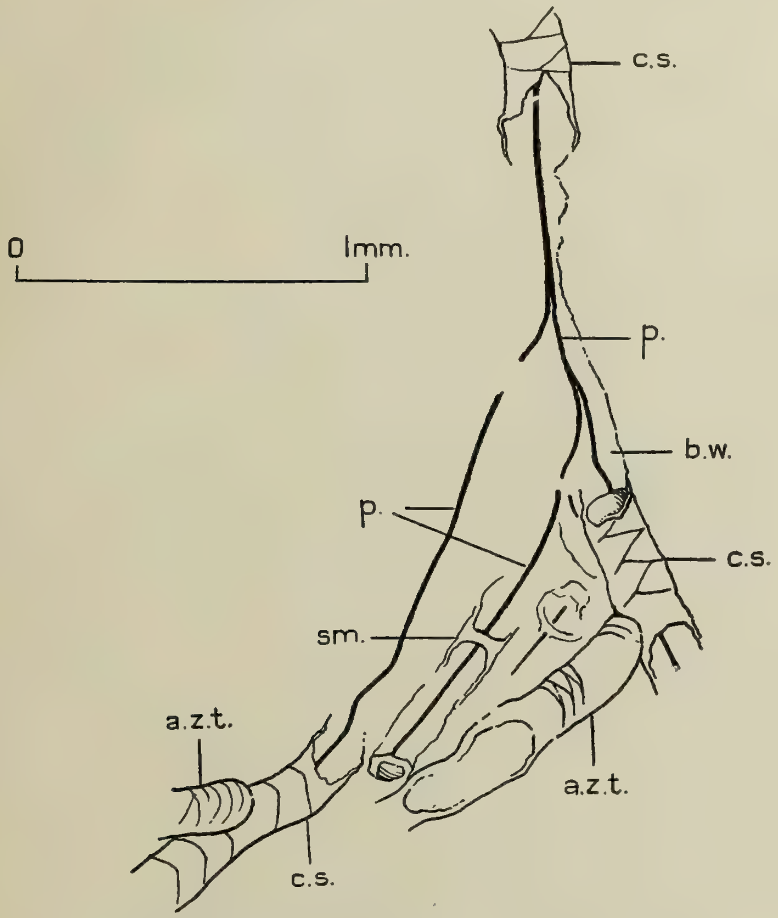
3 *c*. A free part of a zooidal tube showing oblique sutures, H.4170c. (See Pl. 3, fig. 3.)

a.z.t., adherent part of zooidal tube; *c.s.*, creeping stem; *f.z.t.*, free part of zooidal tube; *t.z.t.*, terminal zooidal tube. [*The scale applies to all the figures.*]

Ten were counted in 412 μ of the terminal tube, while 28 consecutive growth-rings, some distorted, were counted in about 1·325 mm. of the free part of a zooidal tube in H.4171a. The sutures are well-marked, sharp, straight ridges, but the extent to which they project could not be determined. Occasionally the oblique suture which interrupts each ring and which marks the junction of its first- and last-formed parts is clearly seen (e.g. H.4170c—Pl. 3, fig. 3, and Text-fig. 3 *c*; and H.4171a—Pl. 2, fig. 2).

Pectocaulus. The pectocaulus is preserved in iron pyrites as a slender rod which has been revealed by weathering of the rest of the coenoecium. In a few instances it shows in a break in the creeping stem (H.4170b—Pl. 2, fig. 4, and Text-fig. 4);

in others it is seen running along the basal wall from which the sides and upper surface of the creeping stem have been worn away; yet again, e.g. H.4171b (Pl. 2, fig. 3), there are instances where only the pectocaulus is preserved on the pebbles.



TEXT-FIG. 4. *Rhabdopleura eocenica* Thomas & Davis
Specimen showing branching of the pectocaulus and its relation to the creeping stems, H.4170b. (See Pl. 2, fig. 4.)

a.z.t., adherent part of zooidal tube; *b.w.*, basal wall of creeping stem; *c.s.*, creeping stem; *p.*, pectocaulus; *sm.*, possible part of a septum. [The tubes in the lower part of the figure were mainly destroyed by decomposition of the iron pyrites after the drawing was made but before they were photographed.]

In a few cases, e.g. H.4170b, the pectocaulus is seen to divide into two (or more) long branches, corresponding to branches of the creeping stem. But there are no indications of short side-branches, so that it seems probable that the adherent parts of the zooidal tubes were without a pectocaulus. The width of the pectocaulus is about 22 μ.

Septum. In H.4170b the pectocaulus traversing the basal wall of a broken creeping stem is interrupted by, and seems to pierce, what appears to be the remains of a vertical wall-like structure within the creeping stem (Pl. 2, fig. 4, and Text-fig. 4). This may be a fragment of a septum though we cannot be certain of this.

REMARKS. It is remarkable that these Eocene specimens of *Rhabdopleura* preserve portions of all the main parts of the coenoecium with the possible exception of the septa, although even one of those may be represented. The external characters of the creeping stem and of the zooidal tubes would alone have sufficed to prove the reference to the genus, but the presence of the pectocaulus is conclusive.

The sutures of the creeping stems and of the adherent portions of the zooidal tubes are generally extraordinarily clear in *R. eocenica*, and are much more easily seen than is usual in Recent specimens. This is almost certainly due to the preservation of the fossils in iron pyrites.

The nature of the relatively short tubes which appear as side-branches of the creeping stems was not obvious at first. The absence of breaks in the upper walls of the latter suggested that the zooidal tubes did not consist only of free, vertical elements which rose directly from them. Instead, it seemed probable that the side tubes represent proximal adherent parts from which the free sections of the tubes developed. As the sutures of the side tubes appeared to be closer together than in the main creeping stems, micrometer measurements were made, and these showed that their distance apart varied between 40 and 55 μ, compared with between 60 and 72 μ for the creeping stems. These results indicated a difference in nature between the two structures, and pointed to the short side-branches being adherent parts of zooidal tubes. This was supported by the upturning and crushing of the distal ends of some of these branches (Pl. 1 and Pl. 2, fig. 1), as though they passed into the upstanding, free parts of the zooidal tubes. Complete confirmation of this was given by the discovery of specimens H.4168b (Pl. 3, fig. 2, and Text-fig. 3 *b*) and H.4170a (Pl. 3, fig. 1), for parts of the free zooidal tubes, with some of their circular growth-rings, are preserved in contact with the adherent parts—the latter show the characteristic, relatively close suturing, and can be seen to spring from creeping stems with the more widely spaced sutures. In H.4170a there are the free parts of at least 10 zooidal tubes, which probably belong to two converging coenoecia.

The crushing of the fragments of the free parts of the zooidal tubes is in striking contrast to the uncrushed condition of the adherent parts of the coenoecia and reflects their vertical growth and more delicate structure. The relative rarity of these free tubes among the fossils is also due to their upgrowing form, for they must have been very liable to damage and destruction, especially after the death of the colony. In the Recent species the free parts of the zooidal tubes also show a similar, rather delicate structure and susceptibility to damage.

IV. COMPARISON WITH OTHER SPECIES OF *RHABDOPLEURA*

Seven Recent species of *Rhabdopleura* have been described, namely, *R. normani* Allman (1869 *a*: 311; 1869 *b*: 439; 1869 *c*: 58, pl. 8); *R. mirabilis* Sars (1872: 1, pls. 1, 2; 1874: 23, pl. 1); *R. compacta* Hincks (1880: 581, pl. 72, figs. 8, 8 *a*, 9); *R. grimaldii* Jullien (1890: 180, text-fig. on p. 181; 1903: 23, pl. 1, figs. 1 *a*, 1 *b*); *R. manubialis* Jullien (1903: 24, pl. 1, fig. 2); *R. striata* Schepotieff (1909: 430, pl. 7, figs. 1–16); and *R. annulata* Norman (1921: 98, text-figs. 3–6). Their characters were summarized by Norman (1921: 96).

The validity of these species is, however, doubtful, for the estimation of what are differentiating characters is a matter of some difficulty. The first five are all Atlantic species. Lankester (1884: 626) interpreted Sars's species as synonymous with Allman's, while later Schepotieff (1907 *a*: 470–471) considered that the five Atlantic species were all one. Broch (1927: 468), van der Horst (1928: 14), and Bergersen & Broch (1932: 16) all agreed that there is probably only one living species, although Norman (1921: 96) considered there were six species at least. Johnston (1937: 6) has accepted the validity of *R. annulata* Norman, but has pointed out 'that peristomes [i.e. free zooidal tubes] of the Tasmanian *R. annulata* when mounted in lactophenol under a cover glass changed their form under the light pressure, losing their markedly serrated margin and becoming very similar to *R. normani*'. Later, however, van der Horst (1936: 535, 586–587), tentatively followed by Dawydoff (1948: 487), recognized three species, namely, *R. normani* Allman, which includes all the Atlantic forms, *R. striata* Schepotieff from Ceylon, and *R. annulata* Norman from Three Kings Islands (New Zealand), Celebes, and Tasmania. We accept this grouping.

R. normani is a very variable species, especially in the characters of the zooidal tubes—sometimes there is no adherent portion, while in other instances it is well developed (e.g. Lankester, 1884: 625–627, pl. 37 *bis*). In its general characters *R. eocenica* is closely allied to *R. normani*, especially to those forms in which there is an adherent part of the zooidal tubes without a pectocaulus, e.g. that described as *R. grimaldii* by Jullien. The fossil species, however, has a narrower creeping stem with more closely arranged sutures, wider growth-rings in the free zooidal tubes, and a more slender pectocaulus.

No specimens of *R. annulata* have been described so far with an adherent portion of the zooidal tubes. The free zooidal tubes appear to be somewhat wider in that species (even in the small Tasmanian form—see Johnston, 1937: 6) than in *R. eocenica*, but the width of their growth-rings is about the same; it is doubtful, however, if the projection of the sutures between the growth-rings in the latter is as great as in Norman's species. The creeping stem in the fossil is narrower also, but the pectocaulus is of the same size as in Johnston's specimens but narrower than in Norman's material (1921: 99), which suggests that the diameter of the creeping stem in any species may vary with the diameter of the pectocaulus.

Although it was not possible to obtain any accurate measurements of the thickness of its walls, they are much thinner in *R. eocenica* than in *R. striata*, while the growth-rings of the free zooidal tubes of the latter are very much wider.

V. ECOLOGY OF *R. EOCENICA*

The genus is widely distributed at the present day, ranging from West Greenland in the north and west to the Antarctic in the south and Three Kings Islands (New Zealand) in the east. It is found living at depths varying from 2 to 550 m. It almost always encrusts some foreign body, e.g. pebbles, corals, ascidians, shells, although the form described as *R. mirabilis* Sars was attached to mud and sand particles and associated foraminiferal tests and shell fragments.

All the specimens of *R. eocenica* known show a similar habitat to that of Recent species of the genus in that they lived adherent to pebbles. The colonies occur mainly on one surface, but they are sometimes present on another also. Traces of the fossil are found on probably 1 per cent. of the pebbles, but good specimens are the exception. The pebbles in the bed yielding the *Rhabdopleura* range from ½-in. to about 9 in. in length, but the smaller and larger pebbles do not seem to have been selected by the colonies as habitats: instead they preferred the medium-sized pebbles, 2 in. to 4 in. in length.

A pebble encrusted with *R. eocenica* frequently shows other adherent organisms, notably:

(i) MOLLUSCA. Oysters of a flat and almost nondescript type are common in all stages of growth. They frequently smother colonies of *R. eocenica*. In these cases the lower valve may often be prised off to reveal the hemichordate. The valves are frequently infilled with iron pyrites.
(ii) POLYZOA. Good healthy growths are found on the pebbles; they frequently grow over a neighbouring *Rhabdopleura* coenoecium. The polyzoa are preserved as casts of the interiors, so that determination of the species is very difficult, only *Dittosaria wetherelli* Busk being specifically recognized. Other forms include *Adeonella* sp., a cribrimorph like *Pliophloea*, and *Aechmella* sp.
(iii) ANNELIDA. *Serpula* sp., as pyritic casts of the interiors of the tubes.
(iv) ANTHOZOA. *Paracyathus* sp., as pyritic casts.
(v) FORAMINIFERA. *Webbina* sp., replaced by pyrites.

This fauna associated with *R. eocenica* is similar to that described for the Recent species. It will be noticed that all of these have lost their calcareous parts with the exception of the calcite shell of *Ostrea*. The only forms truly replaced by the iron pyrites are *Rhabdopleura* and *Webbina*. It is obvious that the pyritization of the chitinous tubes must have occurred soon after the death of the animals for so much of the finer details of the coenoecia to be so well preserved.

VI. THE HEMICHORDA AS FOSSILS

No fossil representative of the class Pterobranchia of the sub-phylum Hemichorda, to which *Rhabdopleura* belongs, has hitherto been described; some authors have even doubted the likelihood of their being found as fossils. In contrast, Kozlowski (1947: 107), then unaware of our discovery, has expressed his expectation that pterobranchs would be found preserved in Mesozoic and Tertiary rocks.[1] He has also recorded (1938: 186, 193; 1947: 106) an undescribed genus of the Cephalodiscoidea from the Polish Tremadocian. The present record is, therefore, important in carrying back the geological history of the Pterobranchia, and indeed of the sub-phylum, a considerable distance. The state of development of *R. eocenica* suggests that *Rhabdopleura* has had an even longer history.

Reference must be made to the graptolites, which have generally been placed in the Coelenterata, although other views on their systematic position have been held by various authors. Recent work, however, has shown that they are almost certainly closely allied to the Pterobranchia. Nearly forty-five years ago, Schepotieff (1905) claimed that the graptolites belong to the same class as *Rhabdopleura*, but, as he completely misinterpreted the structure and development of *Monograptus* on which he based his ideas, his hypothesis was not accepted [e.g. Bergersen & Broch (1932: 30), Decker (1947: 130), and Ruedemann (1947: 46–51, especially 50–51), among recent authors, hold very different views]. In 1938, however, Kozlowski published a preliminary note of his observations on certain Tremadocian dendroid graptolites of Poland, in which he recognized the presence of a system of stolons. He amplified this later (1947: 96–107 particularly), while Bulman (1942; 1945: 11–15) confirmed his observations by recording a similar system in a Caradocian species of *Coremagraptus* as well as in other species (1945: 4–5, 7). Kozlowski showed that this system of stolons is identical in its structure and biological role with the gymnocaulus and pectocaulus of *Rhabdopleura*. When this is taken into account with other similarities between the graptolites and *Rhabdopleura* (e.g. the structure of the graptolite rhabdosome and the coenoecium of *Rhabdopleura*, and the mode of budding of the zooidal tubes of the latter and the development of the first theca of the graptolites), Kozlowski's claim becomes very convincing that there is a close genetic relationship between them, and that the class, Graptolithina, to which the graptolites belong, is very closely related to the Pterobranchia. If this be accepted, then *R. eocenica* takes on an increased importance, as it helps partly to bridge the gap between the last dendroid graptolite in the Carboniferous and the Pterobranchia of modern seas.

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[1] While this paper was in the press, Kozlowski (1949: 1505) recorded a species of *Rhabdopleura* from the Danian of Poland.

APPENDIX

THE LONDON CLAY AT LOWER SWANWICK, HAMPSHIRE

By ARTHUR WRIGLEY

Between 1927 and 1932, when the following observations were made, the London Clay was actively excavated at the Bursledon Brick Company's works at Lower Swanwick, Hampshire, half a mile east of Bursledon tollbridge. The section was cut in a hill-side, facing the Hamble river, between the 50 and 100 foot O.D. contours, the base of the working being below the natural level of the site. The strata rise from south to north, the youngest being found only at the top of the southern excavation and the oldest seen only at the base of the northern end.

SECTION (*in descending order*)

Lower Bagshot Sands (14 ft.):

Brown, sandy loams, somewhat bedded, with much dispersed limonite	8 to 9 ft.
Weathering plane	
Light grey sands	4 ft.
D. Flint pebbles, up to 6 in. long, in grey, loamy sand, with numerous decayed fish-teeth	1½ ft.

London Clay (53 ft.):

C. Grey, sandy clay, weathering brown where it reaches the surface and becoming more clayey below: no fossils seen	25 ft.
Impersistent line of flint pebbles with *Rhabdopleura*	
B. Grey, sandy clay with four lines of septaria	13 ft.
Large septaria, 6 ft. down, have abundant *Turritella*, *Cyprina*, and *Pholadomya* spp.	
A. Grey, sandy clay with numerous fossils	15 ft.
Panopea and *Pitaria* are common at the top. Above a line of tabular septaria, $8\frac{1}{2}$ ft. down, the clay is crowded with very large *Pinna*, *Ostrea*, and *Ficus smithii* (J. de C. Sby.), with a varied molluscan fauna. A rich assemblage of Polyzoa was found upon the large *Ostrea*.	
Bed of black flint pebbles in sandy clay: no fossils seen	4 in.

The bed of flint pebbles, D, taken to be at the base of the Lower Bagshot Sands, yielded a great number of fish-teeth in a most peculiar state of decay which has never been observed in the London Clay. The enamel, which is usually perfect and glistening, was greatly discoloured and corroded, while the roots had become rotten and carious. The species, determined by Dr. E. I. White, are:

Myliobatis 2 species
Lamna verticalis (Ag.)
L. vincenti (Winkler)
Odontaspis cf. *macrota* (Ag.)
Phyllodus sp.
? *Galeus* sp.
Squatina prima (Winkler)
Physodon sp.

FAUNA OF THE LONDON CLAY

A, B, refer to the divisions so marked in the description of the Section. Species without such a prefix were not collected *in situ*.

ACTINOZOA

A. *Graphularia wetherelli* M. Edw. & H.

ANNELIDA

Serpula bognoriensis (Mant.)
A. *S. mellevillei* Nyst & Le Hon [= *heptagona* J. de C. Sby., 1844, *non* Münst., 1835]. The characteristic opercula were found.

BRACHIOPODA

A. *Discinisca* sp.—see Muir-Wood, 1939: 154.

LAMELLIBRANCHIA

A. *Anomia scabrosa* Wood
A. *Ostrea*, a large heavy-shelled species like *O. gigantica* Sol. from Barton.
A. *Pinna affinis* J. Sby., reaching a great size and bulk, up to 9 in. long by 6 in. wide and observed in tabular septaria with its axis vertical and gaping end uppermost. The thick, prismatic, outer layer of the test was sometimes

preserved over the nacreous inner coat, which usually is all that remains of this mollusc. Mr. A. G. Davis found an umbo of this *Pinna* containing several indubitable pearls: the specimen is preserved in the Geological Department, British Museum (Nat. Hist.), L.51117.

A. *Modiolus tubicola* (Wood)—in *Teredo* borings.
B. *'Pecten' corneus* J. Sby. [*corneolus* Wood]
B. *Glycymeris brevirostris* (J. de C. Sby.)
B. *Cyprina planata* J. de C. Sby.
A & B. *Pitaria tenuistriata* (J. de C. Sby. *non* Lam.)
A. *Abra splendens* (J. de C. Sby.)
B. *Pholadomya dixoni* J. de C. Sby.
A & B. *P. margaritacea* (J. Sby.)
B. *P. virgulosa* J. de C. Sby.
A & B. *Panopea intermedia* (J. Sby.)
B. *Cultellus affinis* (J. Sby.)
A. *Corbula globosa* J. Sby. [*wetherelli* Edw. MS.]
A. *Teredina personata* (Lam.), boring radially to the centre of a log of wood—see Wrigley, 1939: 418.
A. Well-preserved faecal pellets on septarian surfaces.

SCAPHOPODA

? *Siphonodentalium* sp.

GASTROPODA

Euspira glaucinoides (J. Sby.)
Sigatica hantoniensis (Pilk.)
B. *Turritella* aff. *terebellata* Lam.
Orthochetus elongatus Wrig.
A. *Tibia sublucida* (Edw.)
Aporrhais sowerbii (Mant.)
A & B. *Ficus londini* Wrig.
A. *F. smithii* (J. de C. Sby.)

Several specimens of the same size show that the distinction between these two species is well founded. Some examples of *F. smithii* attain the great size of 5 in. by 3½ in. diameter.

B. *Galeodea gallica* Wrig.
B. *'Cassis' striata* J. Sby.
B. *Murex subcristatus* d'Orb.
A. *Pollia londini* (Wrig.)
A. *P.* sp., longer than *P. londini*
B. *Streptolathyrus cymatodis* (Edw.)
Euthriofusus transversarius Wrig.
A. *E. crebrilineus* Wrig.
B. *Surculites errans* (Sol.) [*bifaciatus* J. Sby.]
A. *Bonellitia subevulsa* (d'Orb.)

A. *Bathytoma* sp. between *B. granata* (Edw.) and *B. parilis* (Edw.)
A. *Turricula cochlis* (Edw.)
A. *T. crassa* (Edw.)
A. *T. stena* (Edw.)
Ancistrosyrinx gyrata (Edw.)
Eopleurotoma wetherellii (Edw.)

CEPHALOPODA

A. *Nautilus imperialis* J. Sby.

STRATIGRAPHICAL DISCUSSION

The occurrence of the base of the Bagshot Sands above the top of the London Clay at Lower Swanwick brickyard, described above, accords with the Old Series Geological Survey map (sheet 11) of 1858, by W. H. Bristow. The New Series map, sheet 316, colour-printed in 1905, indicates Reading Beds at this spot: this must be an error, for below their supposed outcrop fossiliferous London Clay is now plainly visible.

The Lower Swanwick exposure is naturally to be compared with the sections formerly seen during the construction of the railway from Bursledon to Fareham and particularly with the London Clay of a cutting 4 miles west of the brickyard. These railway exposures were described by Elwes (1888, 1890), whose account and diagram were presented in an improved form by Osborne White (1913: 47–52). The Geologists' Association, guided by W. Whitaker, visited the railway during its construction (Whitaker, 1887: 138) and there is no reason for doubting Elwes's description of the London Clay between Fareham station and the Meon river. Unhappily, Elwes did not give the thickness of the strata he records and there is a discrepancy between the lengths of the Ordnance maps and those shown on Elwes's scale diagrams. It is clear, however, that the base of the London Clay occurs near Fareham station, whence the long cuttings westward show successive beds dipping down to the west until the junction of the London Clay and Bagshot Sands occurs at the level of the railway line on the west side of the Meon valley. Farther west, Whitaker (1902: 10) records the presence of a London Clay Basement-bed close to Swanwick station, while 1¼ miles west of that place the top of the London Clay is now seen in Lower Swanwick brickyard. It seems that the whole thickness of the London Clay is twice exposed just above or below the level of the railway line between Fareham station and Bursledon bridge, with an anticline at Swanwick station and a syncline on the western side of the Meon valley. These undulations are quite credible by their proximity to the major anticline of Portsdown.

The Elwes collection is preserved in the Museum of the Yorkshire Philosophical Society. By favour of its Curator, Mr. R. Wagstaffe, and with the kind help of Mr. G. F. Elliott, it has been possible to examine Elwes's Fareham fossils in London. They most decidedly confirm the conclusion that the Lower Swanwick strata are not represented in the Fareham railway section. Generally, Elwes's material shows that his published list may be received with confidence, but, apart from any mere revision of generic names, the following corrections may be noted, Elwes's determinations being within brackets:

[*Leda substriata* ? Mor.] = *Nuculana oblata* (S. Wood)
[*Ostrea flabellula* Lam.] = *Ostrea multicostata* Desh.
[*Astarte tenera* Sby.] = *Astarte subrugata* S. Wood
[*Turritella imbricataria* Lam.] = *Turritella* aff. *dixoni* Desh.
[*Rostellaria lucida* Sby.] = *Tibia sublucida* (Edw.)
[*Natica labellata* Lam.] = *Euspira glaucinoides* (J. Sby.)
[*Cassidaria nodosa* Sol.] = *Galeodea gallica* Wrig.
[*Pisania sublamellosa* Desh.] = *Pseudoneptunea curta* (J. Sby.)
[*P. morrisi* Edw.] = *Pollia* aff. *londini* (Wrig.)
[*Cancellaria laeviuscula* Sby.] = *Bonellitia subevulsa* (d'Orb.)
[*Pleurotoma* near *wetherelli* Edw.] = *Eopleurotoma simillima* var. *crassilinea* (Edw.)

Two unrecorded species have been found in this material—*Eopleurotoma koninckii* (Edw. *non* Nyst) and *Bullinella* aff. *uniplicata* (J. de C. Sby.). The remarkable feature of this collection is the presence of no fewer than five well-defined species, not merely undescribed but which, so far as I know, have not yet been found in the London Clay of any other locality. They comprise *Arca*, *Sconsia* (a genus new to the London Clay), *Murex* 2 spp., and *Siphonalia*.

A fair idea of the succession of London Clay strata in this locality will be obtained by following Elwes's account from the base at Fareham station upwards to the stiff, blue clay immediately above the two pebble-beds with *Terebratula*, allowing for a probable gap in the record by the interruption of the section at the Meon valley and completing it by the strata seen in Lower Swanwick brickyard here described up to the Bagshot Sands. The total thickness, by analogy with the complete London Clay found in borings at Woolston and at Southampton Common, appears to be about 300 ft. [Whitaker (1887: 138) noted that the Fareham *Terebratula* occurred 'in nests like miniature mussel-banks'. Muir-Wood (1933: 170) has described *Terebratula hantonensis* from the Fareham railway-cutting.]

In comparing the fossil mollusca of the brickyard with those recorded from Fareham, one notices that although many of the gastropoda found in the brickyard occur in the *Terebratula*-bed of the railway and in the sandy clay below it, i.e. beds 2 and 3 of the version by Osborne White (1913: 48), yet there are differences between the two faunas which become significant by the proximity of the sections. The flabelliform *Ostrea*, the *Turritella* of *imbricataria* type, and the *Ditrupa* which was found in masses at several horizons on the railway are conspicuously absent in the brickyard where, also, there is no trace of a *Terebratula*-bed or of the *Dentalium* which occurred commonly in the sands below it. '*Pecten*' *corneus* and two very distinct species of *Pholadomya* are peculiar to the brickyard and are quite common there. Bed A, so notable at Lower Swanwick, with its huge *Pinna*, *Ostrea*, and *Ficus smithii*, is quite different from anything recorded by Elwes.

The comparison of sections of London Clay in the Hampshire basin is a most difficult task. Bognor, Portsmouth, Southampton, Fareham, Whitecliff Bay, and

Alum Bay offer satisfactory records of a complete London Clay, deposited in a shallow sea and presenting the utmost variety and discrepancy, which, at present, defy fruitful correlation.

During the recent war this brickyard was unworked and the section recorded above has become totally obscured by talus and vegetation. Recently, work has been resumed by a new method of excavating clay below the lowest horizon (A) of the earlier workings. Many fossils are to be found and it is hoped that the collection and study of them will fill the gap in a complete, local London Clay sequence noted above to be found in the railway section at the Meon valley.

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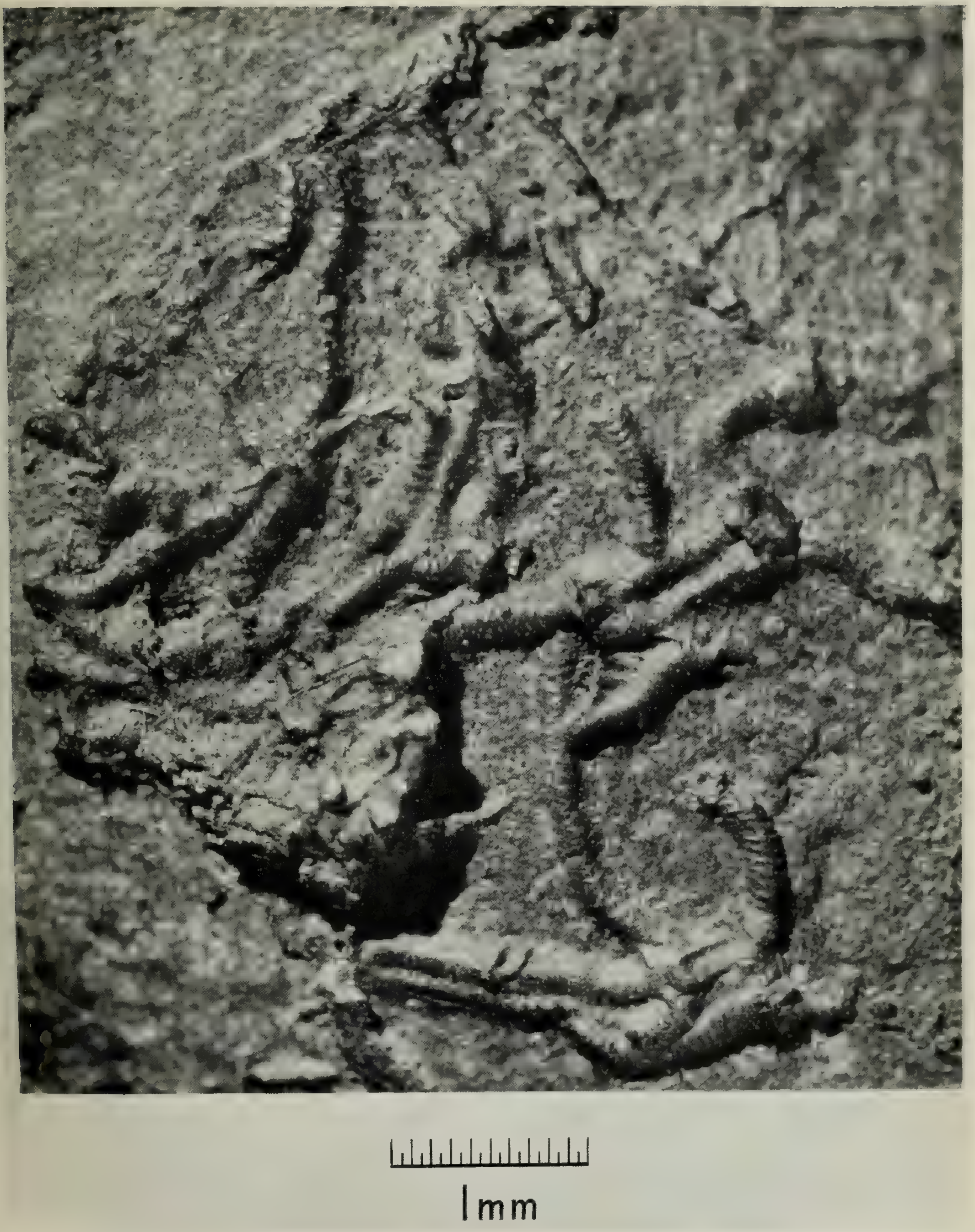
PLATE 1

Rhabdopleura eocenica Thomas & Davis

A series of intersecting coenoecia, H. 4169. Paratype.
See Pl. 2, fig. 1, and Text-fig. 2.



RHABDOPLEURA EOCENICA

PLATE 2

Rhabdopleura eocenica Thomas & Davis

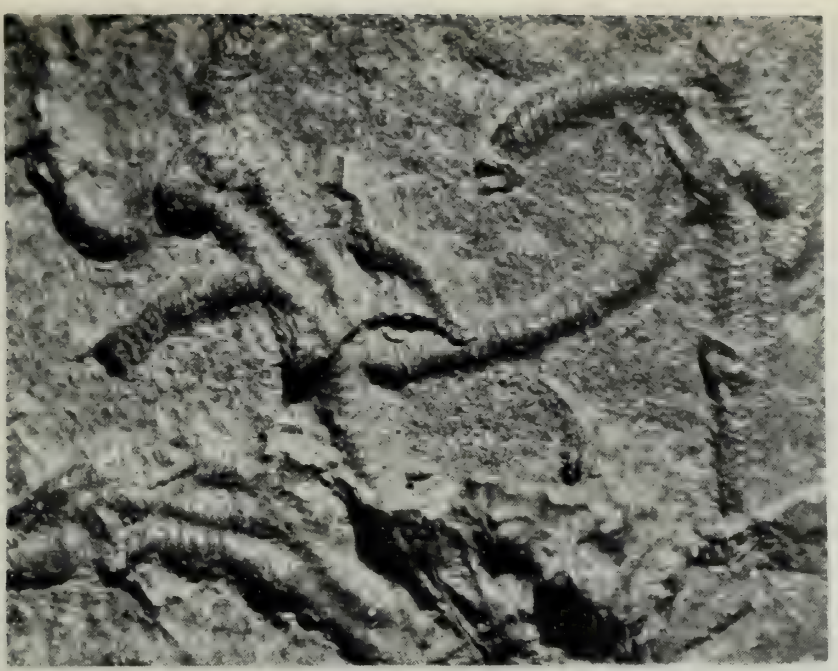
Fig. 1. Another view of part of H.4169 differently lighted to show sutures. See Pl. 1.

Fig. 2. Long free parts of zooidal tubes, H.4171a. Paratype.

Fig. 3. Specimen represented only by a branching pectocaulus, H.4171b. Paratype.

Fig. 4. Specimen with a branching pectocaulus and part of the creeping stem (at top) and creeping stems with zooidal tubes at lower left, H.4170b. Paratype. See Text-fig. 4.

[*The scale applies to all the figures.*]



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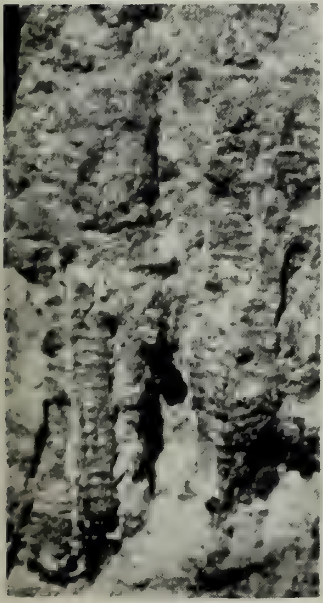

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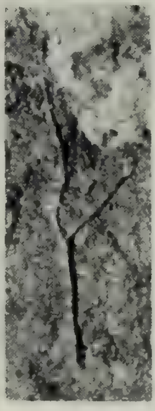

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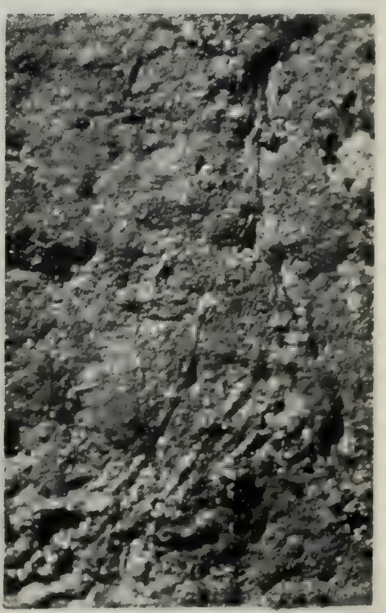

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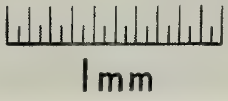


RHABDOPLEURA EOCENICA

PLATE 3

Rhabdopleura eocenica Thomas & Davis

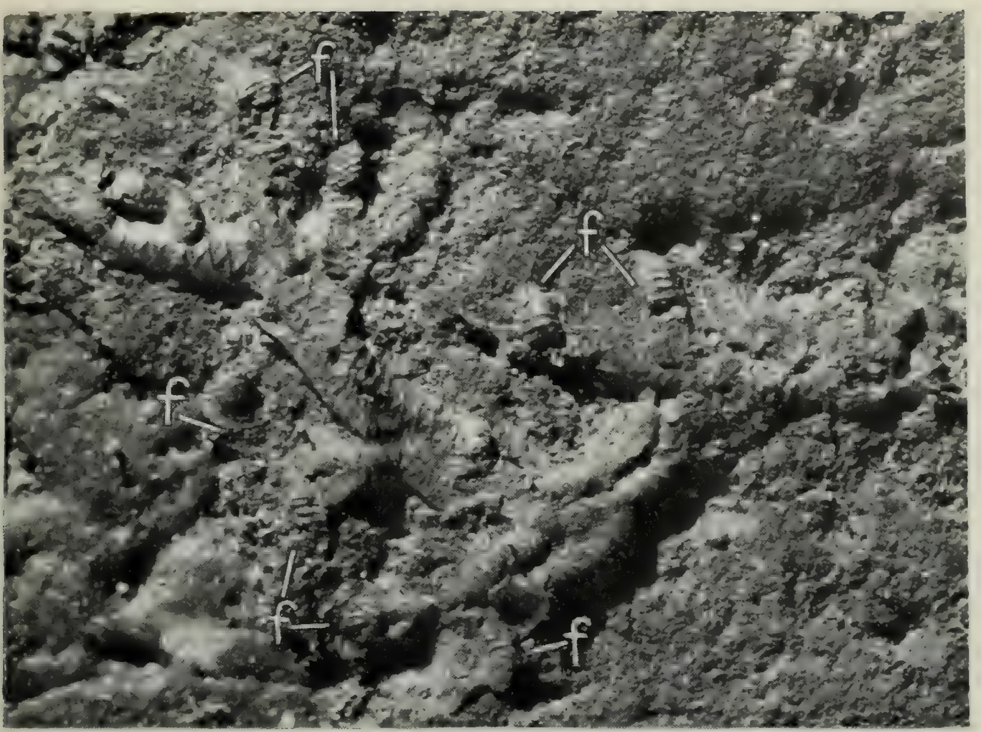
FIG. 1. A number of free parts of zooidal tubes (*f*) in contact with their adherent parts and the creeping stem, H.4170a. Holotype.

FIG. 2. Specimen retaining the adherent and free parts of a zooidal tube in contact with one another and with the parent creeping stem, H.4168b. Paratype. See Text-fig. 3*b*.

FIG. 3. Two isolated free parts of zooidal tubes, the left-hand one showing oblique sutures, H.4170c. Paratype. See Text-fig. 3*c*.

FIG. 4. A creeping stem with an adherent part of a zooidal tube and a portion of the terminal zooidal tube, H.4168a. Paratype. See Text-fig. 3*a*.

[*The scale applies to all the figures.*]



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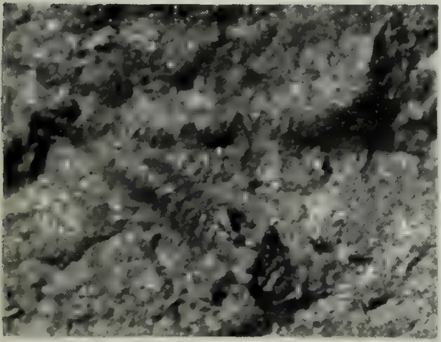

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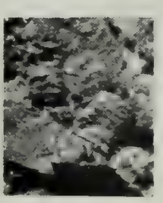

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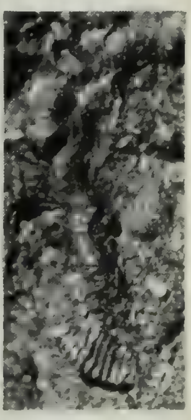

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13 DEC 1949

PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

13 DEC 1949

A RECONSIDERATION OF THE GALLEY HILL SKELETON

K. P. OAKLEY
AND
M. F. ASHLEY MONTAGU

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 1 No. 2
LONDON : 1949

A RE-CONSIDERATION OF THE GALLEY HILL SKELETON

BY

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Pp. 25–48; *Pl.* 4; 4 *Text-figures*

BRITISH MUSEUM NATURAL HISTORY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 1 No. 2
LONDON: 1949

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This paper is Vol. 1, No. 2, of the Geological series.

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THE BRITISH MUSEUM

Issued December 1949 *Price Five Shillings*

A RE-CONSIDERATION OF THE GALLEY HILL SKELETON

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(*With Plate 4*)

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SYNOPSIS

The evidence for the antiquity of the human skeleton found 8 ft. below the surface in gravels of the 100-ft. terrace (Middle Pleistocene) at Galley Hill, Swanscombe, Kent, in 1888 is re-examined. Morphologically the skull and mandible show no features which cannot be matched in the contemporary population of Britain. The probability that the skeleton was interred in comparatively recent times is suggested by the geological evidence, and has been confirmed by application of the fluorine test.

INTRODUCTION

LATE in September 1888 a workman, Jack Allsop, unearthed a human skeleton 8 ft. below the surface when digging gravel in a pit at Galley Hill, on the brow of the 100-ft. terrace overlooking the Thames in the parish of Swanscombe, Kent (Figs. 1 and 2). Matthew Heys, headmaster of the elementary school which adjoins the pit, was brought in to see the skull and other bones protruding from the gravel face shortly after they had been exposed, but school duties prevented him from taking action. It happened that shortly afterwards an amateur archaeologist, Robert Elliott, a printer by trade, from Camberwell, visited the pit and removed the bones, which were in a fragmentary condition. A few days later he took them to London to the palaeontologist, E. T. Newton, who offered to mend and study the material, but Elliott said that he would like to work up the subject and publish his own account of the discovery. However, he was unable to find the necessary leisure and after a lapse of six years Frank Corner, medical practitioner of Poplar, persuaded him to hand the material to Newton for description. In the early years of the present century Corner bought the Galley Hill skeleton from Elliott for £100,[1] and in 1912 deposited the remains on loan in the Department of Geology, British Museum. Here they remained until January 1948, when they were withdrawn by Corner's widow, Mrs. D. H. Pearson, and at the present time they are packed in the store-room of Messrs. Puttick & Simpson, London. Small samples of the bones and of the deposits in which they lay embedded are preserved in the Elliott Collection in the Department of Geology.

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[1] We are informed by one of Robert Elliott's sons (Mr. Arthur Galley Swanscombe Elliott) that Corner thus enabled his father to settle a debt.

HISTORY OF INVESTIGATION

In 1895 Newton presented to the Geological Society of London a detailed account of the skeleton and of the evidence for its antiquity. He pointed out that the skull appeared to represent an extreme form of the Long Barrow race, which typically was Neolithic. But having weighed the evidence he found no reason for disbelieving the statements of Heys and Elliott that the gravel overlying the bones was undisturbed, and in that case the remains were Palaeolithic. However, he phrased his initial conclusions with caution. For instance, referring to his inspection of the site in 1894 he wrote (1895: 520): '. . . the gravel itself, which contained the bones, has been removed, and the present face of the pit is about 10 feet from the exact spot. This change, although slight, is quite sufficient to prevent verification of the undisturbed condition of the gravel overlying the skeleton which, under the circumstances, is so desirable. . . .' But later he said: 'I am not aware of any human bones which have a greater claim than these to be accepted as having been coeval with the Mammoth' (Newton, 1898: 258).

Most geologists and prehistorians have always been sceptical about the alleged antiquity of the Galley Hill skeleton. In the discussion which followed the reading of the paper to the Geological Society (Newton, 1895: 525–7), Sir John Evans said that 'what weighed most with him, and led him to doubt whether the bones were of the same age as the gravels, was the fact that nearly the whole skeleton, including the lower jaw and clavicle, had been preserved'. This, he said, 'was suggestive of an interment'. Boyd Dawkins said that in his opinion 'the skeleton was probably the result of interment in the Palaeolithic gravels at a later time'. He suggested that it should 'be placed to a suspense account'. Sollas 'regretted that the evidence for the absence of interment was not more perfect'.

Many physical anthropologists, on the other hand, apparently impressed by the cogency of Newton's case for the Palaeolithic age of the skeleton, have been inclined to stress such features in the skull as might be interpreted as primitive. Klaatsch (1910) considered that the skull agreed closely with the Combe-Capelle and Brünn (Brno) skulls of Upper Palaeolithic age, the former of which he described as the type of a new sub-species, *Homo aurignacensis hauseri*. In 1911 Sir Arthur Keith was of a similar opinion, but he proposed that the term 'Galley Hill race' should be used to cover all variants of the type. He considered that the Galley Hill specimen was the oldest known representative of the race, which he said had a very long range in time, being 'still represented in the modern population of Britain' (Keith, 1911: 43; see also Keith, 1948: 265).

In 1913 Dr. W. H. L. Duckworth reviewed the evidence for the antiquity of the Galley Hill skeleton and concluded that it was almost certainly a burial, possibly of comparatively recent date. In succeeding years Keith (1915: 184–5) accepted it as a burial, but he maintained that it was interred from a Lower Palaeolithic (Chellean) land surface.

If the geological evidence had indicated an *Upper* Palaeolithic age for the Galley Hill burial, there might have been less scepticism about its authenticity, but at any rate up to a decade ago few anthropologists were prepared to find that modern man dated back to Lower Palaeolithic times. In later years Keith said that he had become 'more and more sceptical of the geological evidence which assigns a high antiquity to modern types such as are represented by Galley Hill man . . .' (Keith, 1930: 30).

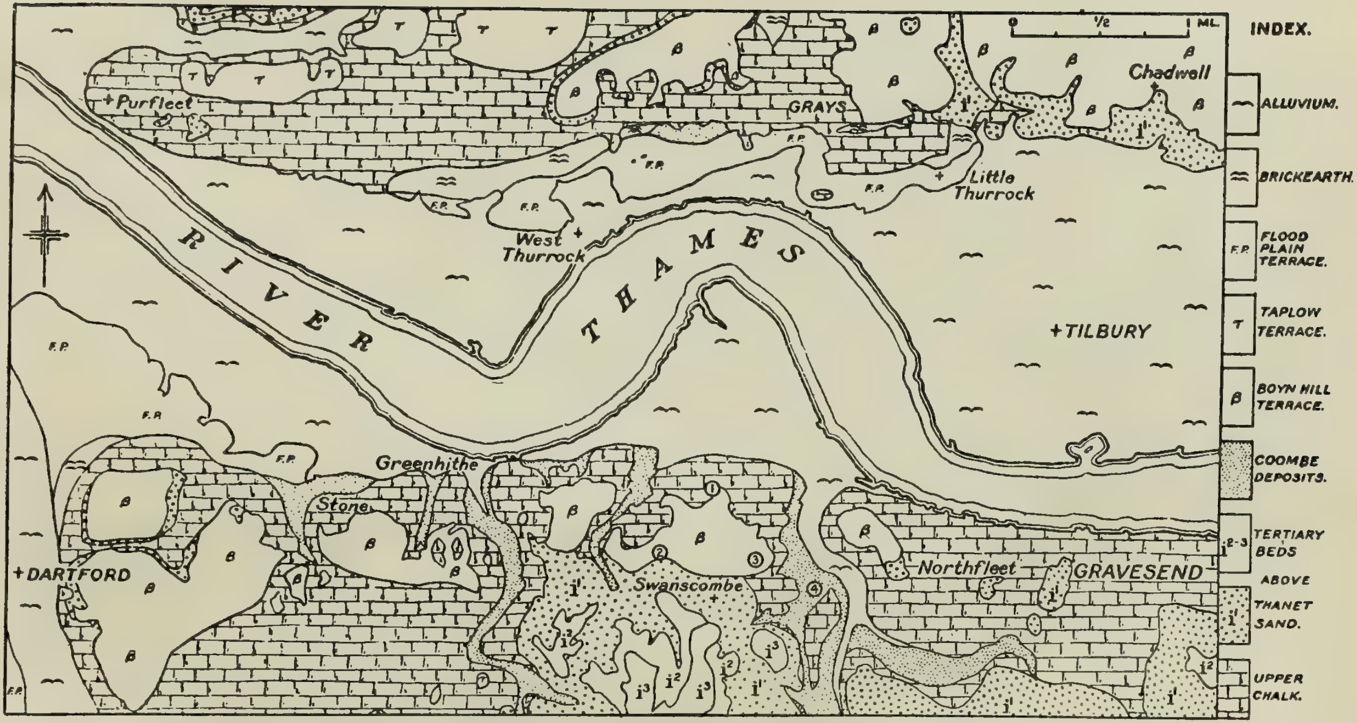
However, in 1935–6 Mr. A. T. Marston discovered part of a human cranium at a depth of 24 ft. in the 100-ft. terrace gravels of Barnfield pit, Swanscombe, not far from Galley Hill (Fig. 1). There was no doubt that this was a fossil skull of Lower Palaeolithic (Acheulian) age. When Professor Le Gros Clark and Dr. Morant (1938) demonstrated that so far as it was preserved it showed no features which distinguished it from modern man, interest in the Galley Hill skeleton naturally revived. At any rate there appeared to be less reason for doubting the antiquity of the latter merely on the score of its modern morphology. Those who had examined the bones, and who were familiar with the geological background of Elliott's find, remained sceptical, but one of the present authors, in common with many others who had to rely solely on published evidence, from then onwards provisionally accepted the Galley Hill skeleton as of Lower Palaeolithic age (Montagu, 1945: 101–3). The current view in the U.S.A. regarding the alleged antiquity of Galley Hill man is that 'a better case can now be advanced than ever before' (Hooton, 1947: 365; see also Coon, 1939: 21).

The possibility of settling debated questions such as this by application of the fluorine test has been under consideration for some years at the British Museum and the present review of the Galley Hill evidence is in fact largely the outcome of a general investigation of the mineral dating of bones which is being undertaken by one of the authors (K. P. O.) in co-operation with staff of the Department of the Government Chemist, London.

In the summer of 1948 the other author (M. F. A. M.) visited England on a grant from the Viking Fund which enabled him to undertake extensive field studies in the Galley Hill–Swanscombe region. While in London he took the opportunity of making a thorough examination of the Galley Hill skeleton in which he had long been interested. When the authors met at midsummer they found that they had independently reached similar conclusions with regard to the probable dating of the skeleton and at the request of the Keeper of Geology they have prepared a joint report on their findings. One author (K. P. O.) has prepared the introductory sections, the account of the geology, and of the fluorine dating: the other (M. F. A. M.) the section on morphology. The sections on conditions of occurrence of the skeleton and on other burials have been prepared jointly. It should be set on record that the conclusions from morphology were reached before the results of the fluorine test were available.

SITE OF DISCOVERY: GEOLOGICAL BACKGROUND

The skeleton was discovered during the removal of gravel overburden from the Chalk, which during the eighties was being quarried from the north-facing bluff of Galley Hill by Messrs. J. B. White, cement manufacturers. This pit had been in use for nearly fifty years and at the time of the discovery the gravels which cap the hill at about 90 ft. above sea-level had already been cleared back to within a few yards of the London road (Figs. 2, 3). Practically all the Chalk thus bared has since been extracted down to the lower limit of working (about 20 ft. above sea-level) and the pit is now disused (Pl. 4 A, fig. 2), but on the south side of the pit, immediately west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T TAPLOW TERRACE.
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COOMBE DEPOSITS.
i2-3 TERTIARY BEDS ABOVE
i1 THANET SAND.
UPPER CHALK.
0
½
1 ML.
Chadwell
+Purfleet
GRAYS
Little Thurrock
West Thurrock
RIVER THAMES
+TILBURY
Greenhithe
Stone
+DARTFORD
Swanscombe
Northfleet
GRAVESEND
F.P.
T
β
i1
i2
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FIG. I. Geological map of part of the Lower Thames area, showing the localities referred to in the text:
I = Galley Hill pit (N), 2 = Barnfield pit, 3 = Rickson's pit, 4 = Baker's Hole (Ebbsfleet).
(Reproduced from Dewey 1932, with slight modification, by permission of the Council of the Geological Society of London.)

of the Galley Hill school and adjoining the London road, there still remains a narrow shelf of unworked Chalk from which it is possible to reach an overgrown section of the gravels close to the site where the skeleton was found. This is the face which was photographed by Clement Reid about 1894 (Fig. 3). In the autumn of 1948 Mr. A. J. Thomas, who until recently was Deputy Manager of the Swanscombe Cement Works (Associated Portland Cement Manufacturers Ltd.), which occupy the floor of this disused pit, kindly arranged to have part of the section cleared so that the deposits could be re-examined (Pl. 4 B).

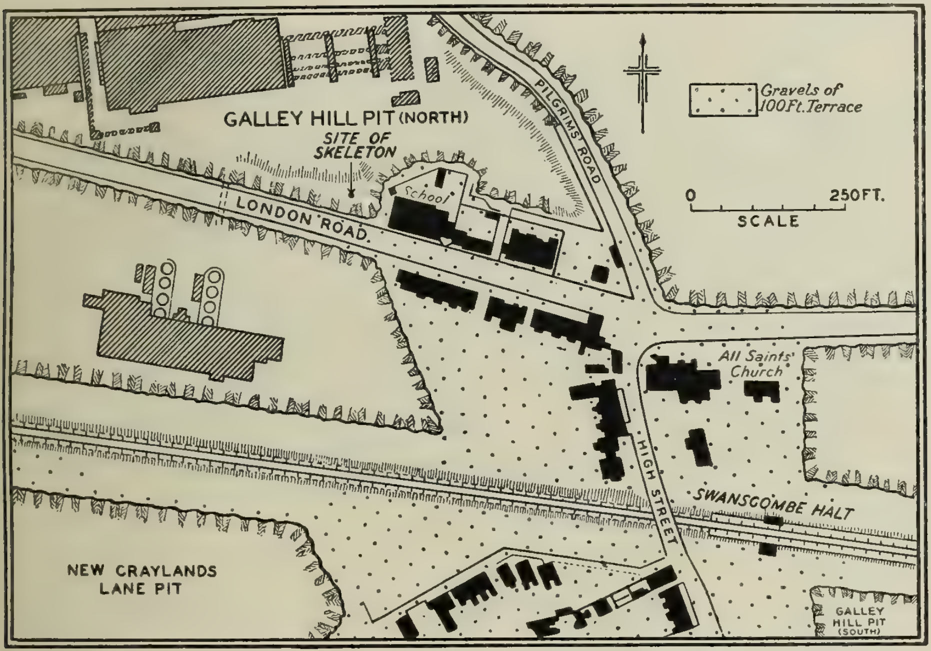

FIG. 2. Map of Galley Hill, Swanscombe, showing present distribution of 100-ft. terrace gravels on the Chalk, and the site where the human skeleton was found in 1888.

(Based on 25-inch Ordnance Survey Map, 1939 revision, and on 6-inch Geological Survey Map 1920.)

The gravels which cap the Chalk on Galley Hill are part of a broad dissected sheet of stratified fluviatile gravels, sands, and loams which belong to the so-called Boyn Hill, or 100-ft. terrace of the Lower Thames (Fig. 1). These deposits attain a maximum thickness of about 40 ft. in the region of Barnfield pit nearly half a mile to the south-west, and they evidently lie within a broad asymmetric channel (Fig. 4) cut partly in Thanet Sand, but mainly in Chalk, trending west to east, and with its deepest portion cut to about 75 ft. O.D. This channel was eroded and then silted-up by the Thames when the river meandered far to the south of its present course, and when the land stood more than 50 ft. lower in relation to sea-level than at the present day. The Chalk floor of the channel rises gently northwards from Barnfield pit, and at Galley Hill, where it is 83 to 90 ft. above O.D., it is covered by only 6–12 ft. of deposits. Undisturbed fluviatile layers have been preserved only over a very limited area at this site, where they are beginning to wedge out against the northern bank of the old channel. Where thin, they have been partly, or even entirely at some points, displaced by unstratified clayey gravel and loam, evidently solifluxion sludge formed under periglacial conditions when the river had abandoned the channel and was eroding its bed at lower levels farther north.

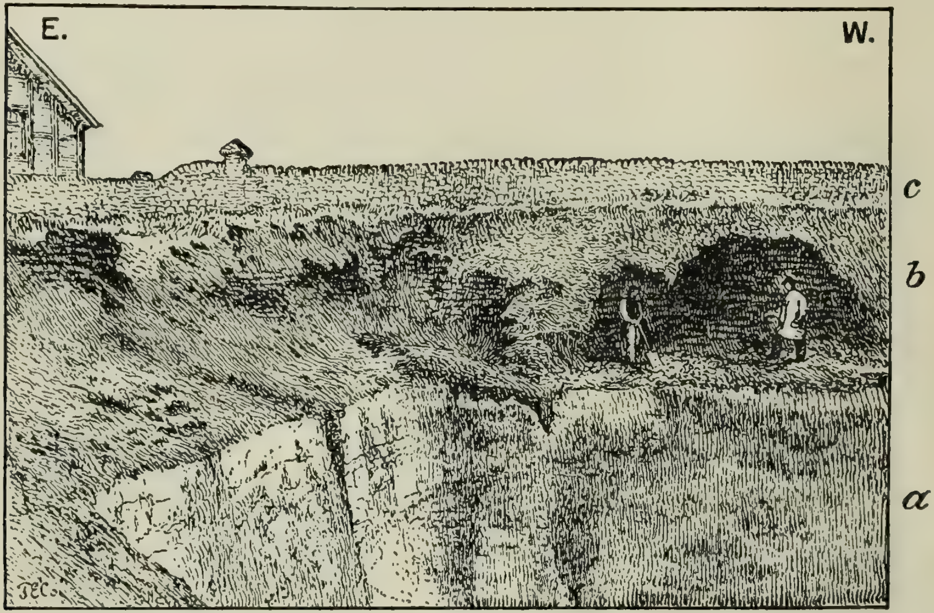

FIG. 3. The Galley Hill pit (North) about 1894. Drawing of the SE. corner of the pit, based on photographs by Clement Reid and J. W. Reed.

a = Chalk, *b* = gravel, *c* = wall flanking London road. The right-hand figure stands on the site where the skeleton was found.

(*Reproduced from E. T. Newton, 1895, by permission of the Council of the Geological Society of London.*)

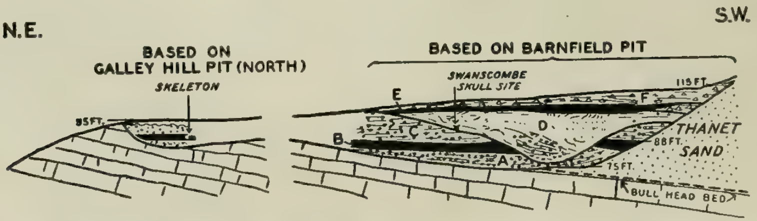
N.E.
S.W.
BASED ON GALLEY HILL PIT (NORTH)
SKELETON
95FT.
BASED ON BARNFIELD PIT
SWANSCOMBE SKULL SITE
115FT.
E
F
D
C
B
A
THANET SAND
88FT.
75FT.
BULL HEAD BED

FIG. 4. Diagrammatic section across the 100-ft. terrace at Swanscombe, showing relative positions of deposits in the Galley Hill and Barnfield pits.

A = Lower Gravel, *B* = Lower Loam, *C* = Lower Middle Gravel, *D* = Upper Middle Gravel and Sand, *E* = Upper Loam, *F* = Upper Gravel.

Not drawn to scale, but figures indicate heights above Ordnance Datum at key points.

(*Barnfield pit based on Dines, 1938.*)

In the critical section west of the school buildings the gravels are sandy and nearly

10 ft. thick (Pl. 4 B). Although disturbed to varying depths by solifluxion and solution piping, they are seen at some points to be well stratified throughout the greater part of their thickness, and are clearly of fluviatile origin. They become thinner, and consequently more confused by solifluxion, to the east and to the west, and die out altogether to the north; so evidently they occupy an embayment in the northern margin of the Swanscombe channel. The section on the far side of the pit, only about 100 yards to the north-east, shows no remnant of these fluviatile layers, only solifluxion gravels with pockets of subaerial loam, resting directly on Chalk.

Although now truncated by quarries on the south side of the London road, the fluviatile gravels of Galley Hill were originally continuous southwards with those exposed in the New Craylands Lane and Barnfield pits (Dines, 1938). In the Barnfield pit (Figs. 1, 4), which is generally regarded as the type-section of the 100-ft. terrace of the Lower Thames, there are four main divisions: Lower Gravel, Lower Loam, Middle Gravels (and Sands), and Upper Loam and Gravel. The Swanscombe skull (*Homo* sp. cf. *sapiens*) occurred at 94 ft. above O.D. in the Middle Gravels. It has been suggested that the Galley Hill skeleton came from a layer corresponding to the Lower Gravel or the Lower Loam (Keith, 1915: 184; cf. Rutot, 1910: 241–3). It is worth considering this possibility, if only as a means of presenting a fuller picture of the deposits with which investigators of the human remains are concerned.

The skeleton was found 2–3 ft. above the base of the gravels. From the published data and from measurements taken in 1948, it is estimated that it was approximately 86 ft. above O.D., which is close to the maximum altitude attained by the Lower Gravel in the region of Barnfield pit. When one considers, however, the way in which the fluviatile deposits of the 100-ft. terrace were laid down, by a meandering, perhaps at times braided, river which was continually carving out new channels and then aggrading them, it becomes obvious that deposits at the same level are not necessarily of the same age. This principle is strikingly illustrated by the section in the Barnfield pit (Fig. 4) which shows the Upper Middle Gravels occupying a channel cut into the underlying deposits down to the base of the Lower Gravel.

It is nevertheless well established that the Lower Gravel and the Middle Gravels are distinct and persistent units in the 100-ft. terrace of the Swanscombe district, probably in origin separated by a considerable interval of time. The Lower Loam, which in Barnfield pit caps the Lower Gravel, shows the weathering characteristic of a land-surface. The two gravels are recognizable, although not separated by an intervening bed of loam, in Rickson's pit, ¾ mile to the south-east (Fig. 1). They are distinguished by totally different Palaeolithic industries. The Lower Gravel contains numerous Early Clactonian flakes and cores (formerly classified as Strepyan or Pre-Chellean) but no bifacial hand-axes. The Lower Loam is archaeologically sterile but clearly belongs to the Lower Gravel stage. The Middle Gravels are rich in unworn Acheulian hand-axes (*bifaces*), including types which were at one time classed as Chellean. It is therefore quite legitimate to inquire whether the Galley Hill gravels belong to the Lower Gravel stage or to the Middle Gravels stage, or, indeed, whether they include condensed representatives of both.

From Elliott's description of the deposits visible in the critical section in 1888, confirmed by Heys's letter to Keith (1915: 181), it appears that the skeleton was partly contained by a seam of loam 2 ft. 6 in. above the base of the gravel. The same or a similar seam (*vide infra*) was visible in 1894 after the section had been worked back 10 ft.; but none was encountered when the section was reopened in 1948. The Lower Middle Gravels in Barnfield pit are covered by an impersistent layer of loamy silt (Marston, 1942: 106), and the Middle Gravels of Rickson's pit also include lenticular seams of loam or clay (Dewey, 1932: 45). There is no evidence to support the suggestion that the seam recorded by Elliott corresponded to the Barnfield Lower Loam rather than to one of the loamy intercalations in the Middle Gravels. Judging from the fact that Elliott's collection from Galley Hill consists almost entirely of Acheulian hand-axes (mainly 'points'), it seems unlikely that the Lower Gravel is represented there at all. Early Clactonian artifacts occur only sparingly. A slightly rolled conical core of that industry was turned out at about 3 ft. above the base of the gravels in the recent excavation, but such specimens could be residue of Lower Gravel eroded from this part of the channel in Middle Gravel times.

On balance the available evidence suggests that the deposits in which the skeleton appeared to lie belong to the Middle Gravel stage, but it must be borne in mind that this in itself represents a lengthy period of time. As already indicated, these deposits are the alluvia of a river which was continually shifting its course and whose volume was liable to considerable variation; swollen by rains and in full spate it would scour channels through older alluvium, and then as the volume slackened these would be filled with fresh deposits. Thus the gravels exposed in different pits at the same general level are likely to vary in age. This is borne out by differences between the assemblages of Acheulian implements from the various exposures of Middle Gravels in the Swanscombe region. Although it is possible that the gravels in the Galley Hill pit are slightly younger than the Middle Gravels in some other sections of the 100-ft. terrace, there is no evidence to suggest that in time of formation they fell outside the limits of the main Acheulian interglacial (Middle Pleistocene). So far as can be ascertained the Galley Hill collection is lacking in twisted ovates and tortoise-cores, types characteristic of the traditions which prevailed during the close of that period, when the Thames was intermittently cutting its bed to lower levels and the climate was becoming periglacial. The even, horizontal bedding of the Galley Hill gravels is indicative of normal fluviatile origin and precludes the possibility that they have been redeposited in a hollow of the terrace by freshets during the melting of frozen ground-water in Upper Pleistocene times. They are river deposits forming an integral part of the 100-ft. terrace, so that if the Galley Hill skeleton is accepted as indigenous, and not a later burial, it would have to be considered as broadly contemporary with the Swanscombe skull.

The dating of the Galley Hill skeleton as Upper Pleistocene by some authorities (e.g. Paterson, 1940: 49, who refers it to a new subspecies *Homo sapiens londiniensis*), is presumably either based on skull morphology, which Professor Montagu shows below to be fallacious, or on the typologically advanced appearance of the supposedly associated hand-axes, which could, however, be accounted for by mere precocity on the part of some of the Acheulian knappers. From the geological evidence it is known that the Thames did not re-aggrade its bed to the 100-ft. level after the downcutting which followed the Middle Gravels stage. Whatever system of classification of Thames terraces is followed, there seems to be no escape from the conclusion that the fluviatile gravels at Galley Hill belong to the same physiographic cycle as those from which the Swanscombe skull was recovered, now generally classed as Middle Pleistocene.

CONDITIONS OF OCCURRENCE

Robert Elliott and Matthew Heys saw part of the skeleton *in situ* before removal. Heys, writing in 1895, seven years after the discovery, said: 'I was struck by the undisturbed condition of the gravel in which it was embedded; it seemed as though gravel and skull were deposited at the same time.' Elliott in a letter to E. T. Newton in 1894 stated the facts, so far as he could remember, as to the conditions under which they were found. The greater part of the letter is quoted by Newton (1895: 518). When Elliott entered the pit in September 1888 on one of his fortnightly visits in search of flint implements, the workman, Jack Allsop, informed him that he had 'found a skull under the gravel' and then 'produced it in several pieces from the base of a pillar of laminated clay and sand, where he had hidden it'. When asked where the rest of the bones were, Allsop 'pointed to the section opposite this pillar, and a few feet away from it, and told me that he had left the other bones undisturbed, for me to see; and there, sure enough, about 2 feet from the top of the Chalk, and 8 feet from the top of the gravel, portions of bone were projecting from a matrix of clayey loam and sand'. He told Elliott that 'several men employed at the works, the master of the neighbouring school, and a clergyman, had seen the skull'. Elliott's letter continued as follows:

> 'The section of gravel was 10 or 11 feet thick, and extended for a considerable distance along the south and east end of the pit; several pot-holes or pipes running from it, deep into the Chalk. I carefully examined the section on either side of the remains, for some distance, drawing the attention of my son Richard, who was with me, and of Jack Allsop, to it. It presented an unbroken face of gravel, stratified horizontally in bands of sand, small shingle, gravel, and lower down beds of clay and clayey loam, with occasional stones in it—and it was in and below this that the remains were found. We carefully looked for any signs of the section being disturbed, but failed: the stratification being unbroken, and much the same as the section in the angle of the pit remaining to this day, but it was then clear and not covered by rubbish as it is now in places, all the "callow" and loam at the top being at that time removed to allow the gravel being got at.'

It appears that the bones were mainly embedded in loam, but that they projected down into the underlying sandy gravel. Heys (in Keith, 1925: 255) said that the underneath part of the skull was 'resting on a sandy gravel'. In an unpublished part of his letter to Newton, Elliott says: 'I should tell you that I have preserved a small box of sand in which the remains were found and shaken out of the bones.' Two boxes were eventually deposited in the Department of Geology, British Museum (Nat. Hist.). One of these, presumably the box referred to in the letter, contains coarse reddish-yellow quartz sand with numerous small flint pebbles mostly less than 10 mm. in diameter. The lime-content and clay fraction of this sample are negligible. Enclosed in the box is a manuscript label signed R. Elliott: 'Sample of Gravel in which I found the Remains at Galley Hill—2 ft. from Bull Head of Chalk.' (The Bull Head bed is a band of large, green-coated flint nodules, sometimes partly embedded in the Chalk, which in this region forms the base of the Thanet Sand; but Elliott appears to be using the term as synonymous with 'eroded surface of Chalk'.) When the section was reopened in 1948 several feet of stratified sandy gravel, matching the sample in the box precisely, were seen to rest on the Chalk (Pl. 4 B). The second box contains lumps of hard loam of pale reddish-brown colour, with the following manuscript label: 'Clay from Galley Hill. Dug out by the late Mr Topley, Mr Newton, Dr Corner, and myself, June 12th, 1894. R. Elliott.' There is a note in the corner of the label: '*3 ft.* B.H.' (presumably 3 ft. above Bull Head). This sample was evidently regarded as identical with the 'clayey' deposit in which the human limb bones had been found seven years previously. It is not a clay, but a coarse silty loam containing scattered quartz grains and an occasional fragment of weathered flint, and in the dry state it is very porous in texture. The rather ill-sorted appearance of the deposit under a lens is reminiscent of some subaerial brickearths, but this is probably an effect of the loss of a limy matrix. Mr. I. W. Cornwall kindly examined it for us in the Geochronology Laboratory, London University Institute of Archaeology. He reports that it has a pH of 6·8 (confirming our impression of complete decalcification), and further that on mechanical analysis it shows the following composition (summarized): sand 19 per cent.; silt 66 per cent.; clay 15 per cent. Some of the sand grains, which are well lustred as in a river sand, exceed 1 mm. diameter. The deposit was evidently waterlaid, but Mr. Cornwall points out that the unusually high proportion of the 'silt-grade' (0·008–0·1 mm.) suggests that it may contain redeposited loessic material.

The finding of a human skeleton embedded in two distinct types of matrix (silty loam and clean gravelly sand) is suggestive of artificial burial. There is, however, a more important consideration which supports this contention. The occurrence of articulated human bones in the Galley Hill deposits would be less surprising if fossil animal remains had been common at the same site, but in spite of the large quantities of gravel removed from the pit no fossil bones have been recorded there. The equivalent gravels in Barnfield and Rickson's pits have yielded quantities of contemporary animal remains (but only very rarely have two or more bones of an individual animal occurred in juxtaposition, even of abundant species such as the fallow deer *Dama clactoniana*). Excavation of about 80 cubic yards of Middle Gravels in Barnfield pit during the summer of 1948 produced over one hundred fragments of bone. The difference in this respect between the deposits in the Galley Hill pit and those in the Barnfield pit is readily explained, but the explanation is not reassuring from the point of view of substantiating the claim that the human skeleton from the former is indigenous. Whereas the Barnfield gravel, sands, and loams are so placed that they have largely escaped decalcification by percolating water, those at Galley Hill have been almost completely decalcified. It might be argued, of course, that the Galley Hill skeleton was protected from the action of percolating water by an impermeable clay matrix, but we have the evidence of the samples preserved by Elliott, which indicates clearly enough that the bones were contained in a permeable deposit. This point does not appear to have been considered by previous investigators, but indigenous bones could scarcely have survived since Middle Pleistocene times in a porous layer within gravels which have undergone complete decalcification. One must conclude, therefore, that the bones were introduced after the deposits had been decalcified.

Some authorities have stated that the preservation of the bones accords with that of other bones from the Pleistocene deposits of the Swanscombe region; but this is not true. The bones were soft at the time of their extraction, and after drying in the air were treated with 'gelatine' and later dipped in preservative solution (Newton, 1895: 519). These treatments have given their superficial surfaces an almost purplish hue, which at first glance gives the appearance of considerable antiquity. However, where the bone has been broken after being 'dipped' the colour is the same as that of the other bones, pale greyish-beige, as in bones of known Holocene age. The bones are light in weight, quite unmineralized, and scarcely different in appearance from those of comparatively recent domestic animals the bones of which one may pick up from the surface in the vicinity of Galley Hill. Although fossil bones of a pale beige colour are found in some Pleistocene brickearths, they are generally distinguished by their greater density or more compact texture. The characteristic fossil bones in the Pleistocene gravels and loams of the Swanscombe region have quite a different appearance, being stained yellowish or reddish brown, and usually showing dendritic stains of manganese oxide.

Newton rejected the possibility that the skeleton had been let down from the surface in a solution-pipe, on the grounds that the cleared area of Chalk showed no trace of a pot-hole immediately below the spot where the bones had been found. Perhaps rather more conclusive as regards this question are Elliott's observations, confirmed by Heys (Keith, 1925: 255), which imply that the containing deposits had the appearance of horizontal beds.

Newton dismissed the other important possibility, that the skeleton was the result of comparatively recent interment, for reasons which are now seen to be inadequate. His whole case rested on the fact that Heys and Elliott detected no signs of disturbance in the overlying gravel; but by the time that they saw the remnants of the skeleton sticking out of the face, it is probable that the bulk of any evidence of burial had already been destroyed by the gravel digger. From our experience of sections at Galley Hill we suggest that the deposits may in any case have been of such a nature that traces of disturbance due to burial would have been obscure (cf. Pl. 4 B). McKenny Hughes (1912: 187) has shown how easily traces of interment are obliterated in Pleistocene deposits; and more than one experienced geologist on first glancing at a section has mistaken settled layers of tipped gravel for natural strata.

Newton argued that simple graves are rarely, if ever, as deep as 8 ft. However, without knowing the precise nature and sequence of the superincumbent beds or the detailed contour of the ground before the gravel was stripped of 'callow', it is by no means certain that the only surface from which interment could have been carried out was as much as 8 ft. above the skeleton. Even if it were certain that the present surface was the only one from which it could have been buried, a depth of 8 ft. would not rule out interment. Professor D. M. S. Watson recovered the skeleton of a modern type of ox 8 ft. below the surface of Pleistocene gravels in a pit near by, in Milton Street, Swanscombe (Sutcliffe, 1913: 16). But is it not more likely that the Galley Hill skeleton represents an interment of Upper Palaeolithic age, antedating, say, only part of the overlying gravel (the top part might have been a Pleistocene solifluxion gravel)? If the skeleton were indigenous to the stratum in which it was found it would be of Acheulian age; but once it is admitted to be an interment there remains no vestige of dating evidence in the record of its occurrence. On the evidence considered so far, it could date from *any* period subsequent to the formation of the containing deposit.

TRACES OF OTHER BURIALS

About 1910 Sir Arthur Keith's attention was called to fragments of another human skeleton which had been found in the gravels of the Galley Hill pit many years earlier—in 1884. According to the recollection of Mr. W. H. Steadman, who had been assistant-master in the Galley Hill school at the time, the bones were found at a depth of about 5 ft. below the surface. When Keith was shown the skull, he pronounced it to be of the same type as that of the 'first' Galley Hill skeleton, but he noted that the bones were thinner and whiter, and his final conclusion was that: 'The evidence on the whole is decidedly against the probability of the second Galley Hill man being of the age of the 100-ft. terrace' (Keith, 1911: 43). At the present time no skull answering precisely to Sir Arthur Keith's description can be traced.

Remnants of presumably another fragmentary skeleton have been reported in the gravels of the Swanscombe district (Duckworth, 1913: 460). About 1912 Mr. J. Bazeley White, jun., of the firm which formerly owned the Swanscombe Cement Works, showed Dr. Duckworth parts of a human skull, with associated lower jaw and vertebrae, which were said to have been found 9 or 10 ft. down in the local gravels. The skull was of modern type, but appeared slightly distorted. The bones were of friable texture and like those of Galley Hill man showed scoring by rootlets. The present whereabouts of these remains is unknown.

The fact that human remains of recent appearance have been recorded on more than one occasion deep in the gravels of the Swanscombe district suggests that the Galley Hill skeleton may be one of a series of rather similar burials.

MORPHOLOGY OF THE SKELETON

The following remains of the skeleton have been preserved and were studied (by M.F.A.M.) in June 1948:

1. The greater part of the calvarium together with lateral and inferior parts of the brain box of the right side.
2. Three small fragments of occipital bone, one showing part of the posterior margin of the foramen magnum.
3. The right half of the mandible with chin and the two premolars and three molars *in situ*. (In some works erroneously recorded as left half of mandible.)
4. Right clavicle with acromial and sternal portions missing.
5. Three small portions of rib.
6. Portion of shaft of right humerus measuring 84·5 mm. in length.
7. Portion of shaft of left humerus measuring 235·0 mm. in length.
8. About half of right acetabulum with small portions of ischium and ilium attached.
9. About half of left acetabulum with portion of ischium.
10. About one quarter of acetabulum with portion of ischium.

11. Right femur complete except for absent greater and lesser trochanteric region. Maximum length 418·0 mm.; vertical diameter of head 33·0 mm.
12. Left femur in same state of preservation.
13. Right tibia with lower part missing as well as portion of superior articular surface; length 250·0 mm.
14. Left tibia with distal portion wanting; length 244·0 mm.

Newton (1895: 505) mentions only one humerus. 'The shaft of the humerus' is what he wrote in his enumeration. Actually the shafts of two humeri were recovered and preserved. From this list of remains it is legitimate to infer that a complete skeleton was actually present at Galley Hill, but that owing to their extreme softness and to the rather haphazard method of excavation, the other parts were lost. As a fair number of the students of the Galley Hill skeleton have pointed out since Sir John Evans originally made the remark in connexion with these remains, the occurrence of a nearly perfect skeleton is suggestive of an interment. Further evidence in support of this suggestion is to be found in the character of the breakage of the bones of the skull, and in the kind of warping which can be matched in many skulls recovered from known burials.

Considerably more of the right side of the skull, including the mandible, is present than of the left side. Furthermore, the warping or torsion of the frontal bones is markedly to the right. These facts strongly suggest that the body lay on its right side and that the weight of the superimposed earth produced the distortion to the right, as well as the greater fragmentation of the bones of the left side. Duckworth, in 1913, had already made out a strong case for the Galley Hill skeleton being a burial largely on the evidence of the distortion. In the light of the present investigation there can be little doubt that it is; moreover, evidence of antiquity is lacking.

From statements in literature it appears that there has been much misconception as regards the morphology of the skull and mandible. It has been stated, for example, that the skull is exceptionally thick, with vault varying in thickness from 10 to 12 mm. Such statements are apparently founded on the comment by Newton (1895: 506) that 'The walls of the cranium are in most parts very thick, the middle of each frontal being as much as 12 mm.' In fact, the skull bones are for the most part rather thin and far from varying from 10 to 12 mm., they vary from 3·9 to 10·0 mm. The following list presents the measurements taken of the thickness of the skull bones at definite anthropometric landmarks. The measurements were made with Ashley Montagu's sliding callipers (1937). The callipers (cranio-cephalometer) were checked for accuracy. For comparison with these measurements, similar measurements were

Landmark or region	*Galley Hill*	*American white skulls*				
At pterion (right side)	3·9	3·0	4·0	3·7	4·0	4·5
10 mm. above opisthocranion	4·0	7·6	9·5	10·0	6·5	9·3
At lambda	7·1	9·4	8·0	7·9	10·0	7·6
At euryon (right side)	8·0	5·2	5·5	4·6	5·0	7·3
At bregma	8·0	7·3	6·0	5·2	6·1	7·6
At stephanion (right side)	10·0	7·4	5·0	4·9	6·7	8·0
'Middle of frontal' (Newton's measurement)	'10·0'	6·0	9·4	5·8	7·4	9·0

made on five American white skulls taken at random from a dissecting-room population. These measurements are shown opposite those of Galley Hill. All measurements are in millimetres.

If we take the measurements of the Galley Hill skull and compare them with the measurements of the American white skull in the final column, it will be seen that at pterion, above the opisthocranion, and at lambda Galley Hill has thinner bones at this region than this particular American white skull. At the four other regions Galley Hill has thicker bones, the advantage being 0·7 mm. at euryon, 0·4 mm. at bregma, 2·0 mm. at stephanion, and 1·0 mm. at 'middle of frontal'.

With the possible exception of the 2·0-mm. difference at stephanion, it will be generally agreed that these are hardly significant enough differences to justify any claims for the exceptional thickness of the Galley Hill skull bones. In brief, it is evident that the thickness of the Galley Hill skull bones falls well within the range of variation of the thickness of the skull bones of the modern white male.

The only remarkable feature of the Galley Hill skull is the rather extensive superior temporal line, but even this is well within the range of variation of modern European crania.

The 'eyebrow ridges' are of the modern bipartite form, and are not more pronounced than they are in numerous Englishmen of the present day.

According to Sir Arthur Keith (1915: 190–1; 1925: 263–4) the shape and size of the mandibular fossa, the largeness of the ear-hole, the small mastoid process, and the extensive area for the attachment of the temporal muscle are 'characters seen on the skulls of primitive races of modern type'. The shape and size of the glenoid fossa and the size of the mastoid process are well within the range of variation of contemporary Englishmen.

When I examined the skull I found the 'ear-hole' to be completely wanting. At least half of the lateral portion of the petrous bone is missing, and there remains not the least trace of the 'ear-hole', the indications being that the whole external auditory meatus and tympanic plate have been lost through partial disintegration. The loose particles of petrous bone submitted for analysis (Table II, p. 44) were insufficient to account for the part which is missing.

As regards the mandible there is no justification for claiming, as has been claimed, that in the ascending ramus a notch is almost absent. A notch is present and originally was almost certainly as deep as in contemporary man. It appears more shallow than it originally was owing to the absence of the tip of the coronoid process, and to the loss of about half of the ascending portion of the ramus and condyle. Newton's dotted-line reconstruction of these parts is inaccurate, for the base of the notch is in fact preserved.

Keith (1925: 264) states: 'The teeth themselves are not large, the total length of the crowns of the three molar teeth being 34·5 mm. The last molar is slightly longer than the second. The width of the molars . . . is less than the length.' My measurements of the length of the individual molars add up to a total length of the three crowns of 33·3 mm., but as will be seen from the following figures I found the second molar to be longer than the third molar, and the breadth of the third molar to exceed its length.

Measurements of the Right Mandibular Molars of the Galley Hill Skull

	Length	*Breadth*
M_3	11·4 mm.	10·5 mm.
M_2	11·4 mm.	10·0 mm.
M_1	10·5 mm.	10·9 mm.

In any event, with respect to the lengths of M_2 and M_3, consultation of Table II in Gregory & Hellman (1926) will show that even in contemporary whites M_3 is frequently larger, antero-posteriorly, than M_2.

Antero-Posterior Lengths of Lower Molars 2 and 3 in which M_3 exceeds M_2 in Length

(From Gregor & Hellman, 1926)

	M_2	M_3
Indian	11·0	11·5
Hindu	10·1	11·5
Indians	10·8	10·9
White males	9·7	10·0
White females	8·7	9·2

These represent the minimum measurements. The averages for males were M_2 10·7, M_3 10·1; for females M_2 10·0, M_3 9·9.

The teeth show some other features which are of interest. The first and second molars present evidence of what may have been caries. The first molar presents such evidence on the antero- and postero-lingual cusps down to the root distally, while the second molar shows evidence of possible caries in the lingual wall and lingual occlusal surface of the crown. The canine tooth was lost *post mortem*. The appearance of the incisor sockets suggests that the incisors may have been lost *ante mortem*. There is evidence suggesting the presence of some inflammatory condition all the way down to the mentale, with some loss of bony tissue at the chin.

It is evident that none of the features existing in the Galley Hill remains, alone or in combination, would be difficult to duplicate in contemporary human skeletons. There are several features which are rather unusual, but these were almost certainly peculiar to this individual. For example, the right clavicle is very remarkably flattened antero-posteriorly, so that the body presents an almost quadrilateral form in cross-section. This type of flattening appears to have affected several of the long bones, the dorsal surfaces of both humeri, and the shafts of both tibiae. The femora are not markedly affected.

To conclude, then, on morphological grounds there is no reason to consider that the Galley Hill skeleton presents any primitive features whatever. So far as fossilization is concerned, the evidence is largely negative, the bones might be any Quaternary age, but in general their appearance is post-Palaeolithic rather than Palaeolithic.

RESULTS OF FLUORINE TEST

It has long been known that buried bone accumulates fluorine in course of time (Middleton, 1844). Carnot (1893) analysed a large number of fossil animal bones and teeth from various geological horizons, and showed conclusively that as a general rule their fluorine-content increased with geological age. The reason for this is now known to be that bone is partly composed of hydroxyapatite, a form of calcium phosphate which acts as a natural trap for wandering ions of fluorine, the gaseous element present in minute traces in most ground-waters. Fossil bones are rarely screened completely from a slowly moving aquatic medium, and the ultramicroscopic crystal units of the component hydroxyapatite are converted one by one into fluorapatite. This is a stable mineral, resistant to weathering, so fluorine is not readily leached after it has become fixed in bone, and on balance the proportion increases with passage of time. (There are, of course, conditions of weathering which lead to the solution of fluorapatite, but under these the bone itself would not survive.) Owing to the porosity of bone the alteration is not confined to the surface but normally proceeds more or less uniformly throughout the body of the material.

The summary figures published by Carnot, showing the proportions of fluorine characteristic of bones of different geological ages, were based on averages. So many variables are involved that it is patently impossible to date any particular bone merely by determining its fluorine-content. In one locality fluorine may be abundant in the ground-water, while in another it may be a rare trace. Thus, a Pleistocene bone from a site in a fluorine-rich region may have acquired as much fluorine as an Eocene specimen preserved in a F-deficient environment. For this reason Carnot's results have generally been regarded as interesting, but without practical application.

However, it has been pointed out (Oakley, 1948) that if one is dealing with two groups of bones from a given site or area, it should be possible in some cases to determine whether they are approximately contemporary, or whether one is significantly younger, by comparing their fluorine-contents. Such a 'fluorine test' has an obvious application where human remains have been found in a Pleistocene deposit and there is room for doubting whether they are indigenous or have been buried in the deposit in post-Pleistocene times.

With the object of exploring the possible applications of this test, Mr. R. H. Settle and his colleagues Dr. C. R. Hoskins and Mr. E. C. W. Maycock of the Department of the Government Chemist have determined the F-content of a series of minute samples of bone selected by the author. The work is still in progress, and a detailed account, including a description of the method of analysis, will be published at a later date. The results to hand are sufficient to indicate that the test is reliable for determining within broad limits the relative antiquity of bones from a given site, so long as they are preserved in permeable matrices. As expected it is not applicable to the determination of the relative antiquity of bones from widely separated sites, or from deposits of markedly different permeability. (Thus, an Early Bronze Age skeleton buried in *sand* at Walton-by-Felixstowe, in a relatively fluorine-rich area, was found to have accumulated over three times as much fluorine as the Palaeolithic skull preserved in *clay* at the Lloyd's site, London.)

The fluorine test is applicable to the Galley Hill skeleton in view of the fact (which has emerged from our review of the evidence) that the bones were embedded in a permeable matrix. The five small samples of the skeleton which are preserved in the Elliott Collection at the British Museum (Nat. Hist.) were accordingly submitted for F-determination, together with samples of twenty-two bones from various deposits in the Swanscombe region whose approximate relative ages are known. The comparative samples were carefully selected with the object of representing the greatest possible variety of conditions of preservation. The results, which are set out in Tables I and II, give striking confirmation of the conclusion that the Galley Hill skeleton, far from being Middle Pleistocene, is a comparatively recent burial. On the other hand, the known antiquity of the Swanscombe skull has been confirmed by the fluorine test (Table I, items 10–11).

It was necessary, of course, to consider the possibility that the Galley Hill bones are low in fluorine through some of their original hydroxyapatite having been replaced before F-fixation began. However, there is no evidence of ferrugination or other mineralization, and comparison of their F/P_2O_5 ratio with that of the Middle Pleistocene bones on the one hand, and of Holocene bones on the other, shows that their low F-content can be safely attributed to lack of antiquity. The following analytical figures may be taken as representative.

	F%	P_2O_5%	*Iron* (*as* Fe)%
Middle Pleistocene bones			
Sample No. 7 (S37) . . .	2·0	30	1·4
Sample No. 11 (S17) . .	*c.* 2·0	*c.* 27	*c.* 1·5
Holocene bones			
Sample No. 21 (S23) . .	0·3	28	< 0·1
Galley Hill skeleton			
Sample No. 26 (S9) . . .	0·4	27	< 0·1

It is particularly noteworthy that the ranges of F-content in the three age groups (Table I) show no overlap, in spite of the variation in conditions of preservation. Thus, in the Middle Pleistocene bones the average F-content ranges from 1·7 to 2·8 per cent.; in the Upper Pleistocene material the recorded range is 0·9 to 1·4 per cent.; and in the Holocene group 0·05 to 0·3 per cent. As one would expect, there is variation in the F-content of bones within a single deposit, and similarly between one part of a bone and another part; but the ratio of the extremes of this variation does not usually exceed 2. (The variation within an individual bone has a bearing on sampling technique which will be considered in the final report on the fluorine-dating.) If compared with a longer series of determinations, the F-content of the Galley Hill skeleton (average 0·34 per cent.) might prove to fall within the extreme limits of an Upper Pleistocene range; but already, even on the basis of comparison with a very small series of samples, it is practically accommodated by the recorded Holocene range. Thus the figures available are sufficient to indicate that while an uppermost Pleistocene date for the burial of Galley Hill man is not entirely ruled out, an early Holocene date has greater probability.

In concluding this section it is worth setting on record that on being informed of the results of the fluorine test applied to the Galley Hill skeleton, Sir Arthur Keith made the comment that they 'confirm my established doubt' (*in lit.* 22 Sept. 1948; cf. Keith, 1948: 265).

SUMMARY OF CONCLUSIONS

It has been claimed that the human skeleton found in the Middle Pleistocene gravels at Galley Hill, Swanscombe, was an indigenous fossil and therefore of Lower

TABLE I. *Comparison of Fluorine-contents of Bones from Middle Pleistocene, Upper Pleistocene, and Holocene Deposits in Swanscombe Region, Kent*

MIDDLE PLEISTOCENE BONES

Sample No.	*Description of material*	*Register No.**	*Matrix*	*Geological horizon*	*Locality*	*Fluorine %*
1. (S1)	Humerus, *Dama* cf. *clactoniana* (Falc.)	G.D. M16500	Sandy gravel	Lower Gravel, 100-ft. terrace	Barnfield pit	2·0
2. (S2)	Root of incisor, '*Cervus*' sp.	G.D. M16499	Sandy gravel	„ „	„	2·8
3. (S36)	Vertebra, *Dama* cf. *clactoniana* (Falc.)	G.D. M16511	Sandy gravel	„ „	„	2·1
4. (S16)	Humerus, *Felis* cf. *leo* Linn.	G.D. M16501	Loam	Lower Loam, „	„	1·7
5. (S20)	Phalange, *Felis* cf. *leo* Linn.	G.D. M16502	Loam	? Lower Loam, „	Near Swanscombe	1·7
6. (S3)	Metapodial, *Dama* cf. *clactoniana* (Falc.)	G.D. M16510	Sandy gravel	Middle Gravels, „	Barnfield pit	2·3
7. (S37)	Rib, bovine	—	Loam	'Silt layer', Middle Gravels, 100-ft. terrace	„	2·0
8. (S18)	Limb-bone, bovine?	—	Sandy gravel	'Skull level', Middle Gravels, 100-ft. terrace	„	2·0
9. (S19)	Rolled piece of bone, indeterminate	—	Sandy gravel	„ „	„	1·7
10. (S4, 5)	Occipital, *Homo* sp.	G.D. M15709	Sandy gravel	„ „	„	*c.* 1·9
11. (S17)	Parietal, *Homo* sp.	G.D. M15709	Sandy gravel	„ „	„	*c.* 2·0

UPPER PLEISTOCENE BONES

Sample No.	*Description of material*	*Register No.**	*Matrix*	*Geological horizon*	*Locality*	*Fluorine %*
12. (S13)	Skull, *Rhinoceros antiquitatis* Blum.	G.S.M. 4950	Chalky gravel?	'Coombe Deposits'	Baker's Hole	1·0
13. (S14)	Skull, *Rhinoceros antiquitatis* Blum.	G.S.M. 4950	Chalky gravel?	„	„	1·2
14. (S29)	Vertebra, *Megaceros* sp.	L.M. 49.21/1	Loam	Lowermost Loam, Ebbsfleet Series	„	1·4
15. (S25)	Mandible, *Elephas primigenius* Blum.	L.M. 49.21/2	Chalky gravel	Above Lowermost Loam, Ebbsfleet Series	„	0·9
16. (S31)	Limb-bone, ? *Rhinoceros* sp.	—	Loam	Temperate Bed, Ebbsfleet Series	„	1·1
17. (S35)	Ulna, *Rhinoceros antiquitatis* Blum.	G.D. M5137	Loam	Crayford Brickearth, 50-ft. terrace	Crayford (W. of Dartford)	1·0

HOLOCENE BONES

Sample No.	*Description of material*	*Register No.**	*Source*	*Fluorine %*
18. (S12)	Root of premolar, *Ovis aries* Linn.	Z.D. 1949.3.18.1.	Soil, above gravels, Barnfield pit, Swanscombe	0·1
19. (S11)	Skull, *Homo sapiens* Linn.	Marston Coll.	Under collapsed Thanet Sand (dene-hole?), Kemsey's pit, Swanscombe	0·1
20. (S22)	Skull, *Homo sapiens* Linn.	Z.D. 1949.3.9.2.	Chalky soil, Bevan's Works, Northfleet	0·2
21. (S23)	Skull, *Homo sapiens* Linn.	Z.D. 1949.3.9.1.	Chalky soil (said to contain Romano-British pottery), Bevan's Works, Northfleet	0·3
22. (S38)	Tibia, *Homo sapiens* Linn.	Gravesend Library Coll.	Saxon grave, 3 ft. deep in gravel, Northfleet	0·05

TABLE II. *Fluorine-content of the Galley Hill Skeleton*

Sample No.	*Description of material*	*Register No.**	*Matrix*	*Fluorine %*
23. (S36)	Petrous bone of skull	G.D. E1359	Gravelly sand and loam	0·3
24. (S7)	Cancellar tissue of mandible	G.D. E1360	„	0·4
25. (S8)	Right tibia	G.D. E1363	„	0·4
26. (S9)	Loose fragment of limb-bone	G.D. E1362	„	0·4
27. (S10)	Left femur	G.D. E1361	„	0·2

* Key to register numbers: G.D. = Geology Department, British Museum (Nat. Hist.); G.S.M. = Geological Survey Museum; L.M. = London Museum; Marston Coll. = Mr. A. T. Marston's private collection; Z.D. = Zoology Department (Osteology), British Museum (Nat. Hist.). (Unregistered fragmentary bones were used when the matrix and horizon were certain.)

Palaeolithic (Acheulian) age. The skull has been described as showing primitive features conformable with great antiquity.

From the statements of some authors it might appear that the skull is exceptionally thick, but re-measurement has shown that the bones are well within the range of variation found in modern whites, and at some points unusually thin. The eyebrow ridges are not more pronounced than in many Englishmen of the present day. It has been stated that the mandible is of primitive type, and that the sigmoid notch is almost missing. Re-examination has revealed no primitive features; the shallow appearance of the notch is due to the loss of the tip of the coronoid process and of the posterior half of the ascending ramus.

Even the most fragmentary skeletal remains of Palaeolithic man are excessively rare in fluviatile deposits. With the exception of deliberate burials (and the earliest of these are Upper Pleistocene) the association of the skull and limb-bones of a single individual has not hitherto been recorded in undoubted river gravels anywhere in the world. The published claims that this skeleton was indigenous rest on negative evidence. The collector declared that the overlying beds showed no signs of having been disturbed; but by the time he examined the section evidence of burial would have been largely—perhaps entirely—removed by the workman digging the gravel. Some accounts of the discovery give the impression that the bones were contained by a definite horizontal seam of loam within the gravels, but the indications are that their actual matrix was of a mixed character.

Wherever the Swanscombe gravels have been protected from intensive decalcification, as in the neighbouring Barnfield pit, they have yielded numerous fragmentary animal remains. However, in the Galley Hill pit the gravels and intercalated loams have been almost completely decalcified, and so far as is known have never yielded any fossil animal bones or shells. The preservation of the human skeleton (which, it is important to note, was in a permeable matrix) is only accountable as an interment subsequent to the decalcification of the deposits. Traces of two apparently similar burials in the Swanscombe gravels are on record.

The fluorine-content of bones increases with geological age. Comparison of the F-content of the Galley Hill skeleton with that of twenty-two bones of known relative ages from various deposits in the same district confirms the conclusion that it was not indigenous to the Middle Pleistocene gravels in which it lay, but a burial of later date—prehistoric, but probably post-Pleistocene.

ACKNOWLEDGEMENTS

We wish to thank the Trustees of the Viking Fund and of the Percy Sladen Fund for grants which enabled us to carry out various field studies in the Swanscombe region during 1948, which had a useful bearing on the problem of Galley Hill man. In the course of this work we greatly benefited from the courtesy and helpfulness of the staff of the Associated Portland Cement Manufacturers in the Swanscombe district, and in particular we should like to mention our indebtedness to Mr. A. J. Thomas, Manager of Johnson's Cement Works, Greenhithe (and, before that, Deputy Manager of Swanscombe Works).

The section of this report dealing with the fluorine test is entirely the outcome of

the facilities afforded by the Government Chemist, and of the generous co-operation of the members of his staff, Mr. R. H. Settle, Dr. C. R. Hoskins, and Mr. E. C. W. Maycock, and we wish to record our gratitude to them for their valuable contribution to the work.

Finally we would thank many friends and colleagues who have assisted our investigations in one way or another, especially Mr. and Mrs. P. Curnow who were responsible for some phases of the field work; Mr. B. E. Bryant of the Kent Education Committee for inquiring the whereabouts of the 'second' Galley Hill skull; Mr. W. F. Grimes of the London Museum, Mr. R. V. Melville of the Geological Survey Museum, Mr. A. T. Marston and Professor F. E. Zeuner, who provided samples for fluorine analysis; Mr. L. E. Parsons and Mr. S. Ware for their help in the preparation of the samples; and Mr. I. W. Cornwall for reporting on the Galley Hill loam.

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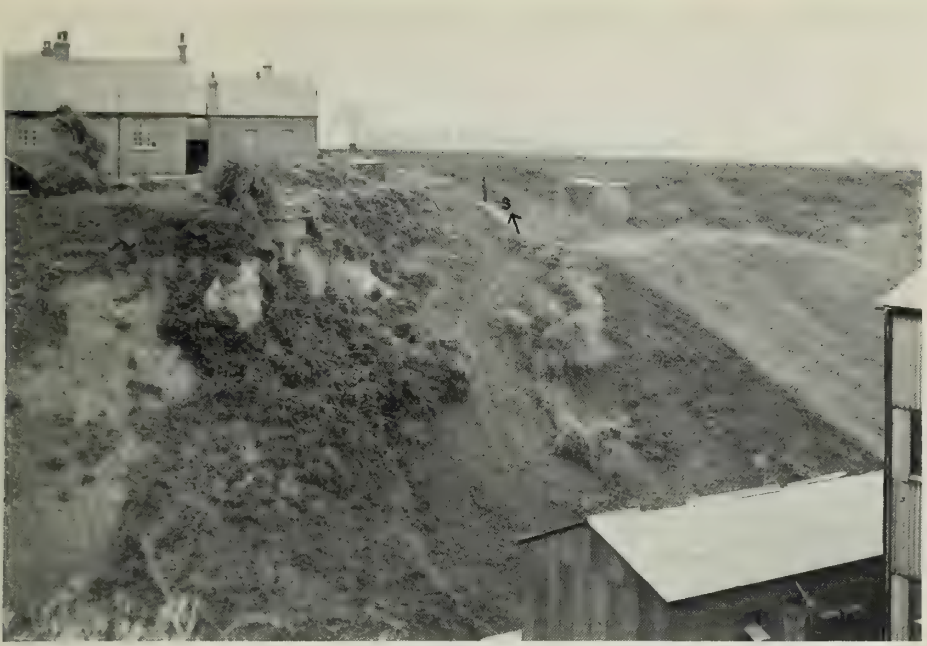
PRESENTED

PLATE 4

THE GALLEY HILL SITE

A. The Galley Hill pit: south side viewed from Pilgrims' Road, looking SW., in November 1948. The site of the skeleton is indicated by *S* on the Chalk shelf to the right of the school buildings. Cf. Fig. 3.

B. Section close to the site showing stratified river gravel on an irregular surface of Chalk. The hand-pick (length 1 ft. 5 in.) is at junction of disturbed and undisturbed gravel, not readily defined.



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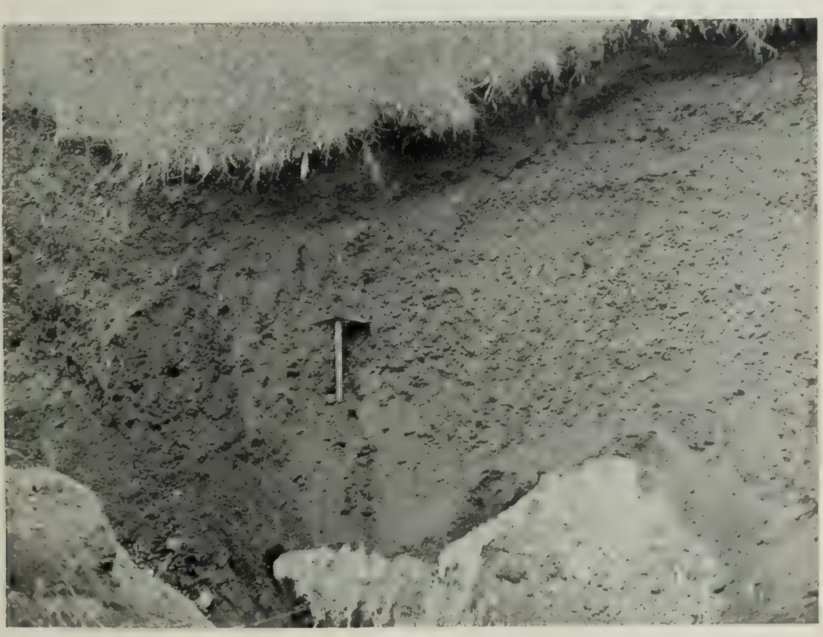

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THE GALLEY HILL SITE

PRESENTED
13 DEC 1949

PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

THE VERTEBRATE FAUNAS OF THE LOWER OLD RED SANDSTONE OF THE WELSH BORDERS

PTERASPIS LEATHENSIS White A DITTONIAN ZONE-FOSSIL

ERROL IVOR WHITE

BULLETIN OF
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY) *instituted in 1949, is to be issued in five series, corresponding to the five Departments of the Museum.*

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These papers form part 3, vol. 1 of the Geological series.

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

31st.
Issued January 1950 *Price Seven shillings and sixpence*

THE VERTEBRATE FAUNAS OF THE LOWER OLD RED SANDSTONE OF THE WELSH BORDERS[1]

By ERROL IVOR WHITE

SYNOPSIS

An account is given of the vertebrates, chiefly Ostracoderms, from the 'Passage Beds' and Old Red Sandstone of the classical area of the Welsh Borders, with details of the localities from which they have been obtained. It is shown that these fossils may be used for zoning the Downtonian and Dittonian rocks over a considerable area, and tentative efforts are made at correlation with other areas. Both the series mentioned are re-defined and the question of the Silurian–Old Red Sandstone boundary is discussed, with a full account of the controversy concerning it, and argument is put forward for fixing it at the Ludlow Bone-bed.

INTRODUCTION

The immediate purpose of this communication is to demonstrate that in the Anglo-Welsh area the strata between the Ludlow rocks and the Carboniferous, especially those below the Brownstones, may be zoned, at least tentatively, on the basis of their vertebrate fossils. This is not, however, merely a question of a local succession but has a far wider significance, for in this region is the type-area of the Silurian System and the 'Passage Beds', and until some such sequence is proven, not only will correlation with Continental and other areas be unsatisfactory but the important question of the Silurian–Old Red boundary must remain in doubt. Emphasis is of necessity placed on the vertebrate fossils which in these generally barren rocks provide by far the commonest remains over much of the area and in all but the lowest members of the succession (cf. Straw, 1930).

Elles & Slater (1906) used invertebrate fossils for zoning their 'Highest Silurian' strata in the Ludlow district, but this work only affected the Temeside Series comprising not more that 170 ft. of rock in the area concerned. Jones (1929: 120A) added two vertebrate zones to cover the succeeding 'Red Downtonian', some 2,000 ft. of rocks, an upper zone of *Tolypaspis* and *Cyathaspis*, and a lower zone of *Auchenaspis* (*Thyestes*) and *Didymaspis*, but a glance at the distribution of fossils given in Text-fig. 1 shows that this arrangement is not possible (the range of *Tolypaspis* is not shown as it is not clearly defined). But the first major effort to divide the whole series of these much-disputed rocks was made by Wickham King (1925, 1934), whose results, however much it may seem necessary to modify them in the light of new knowledge, must always remain the basis for any work of this nature. As I have already pointed out (White, 1946: 208), the stages into which King divided his Downtonian and Dittonian strata are 'lithological in conception and the palaeontological names which have been applied to some of them are based on maximum occurrences of fossils that may be of relatively local significance'. In that paper the case of the '*Psammosteus*' Limestones was dealt with, and it would not be difficult for one reason or another to find fault with the naming of a number of these stages: for example, *Ischnacanthus*, the name-fossil of stage I. 6, is recorded by King himself (1934: 530–1) from below the Ludlow Bone-bed to the Dittonian and is not uncommon in beds reputed to be in stage I. 8; while there is evidence that the sandstones and cornstones which yield rich harvests of *Cephalaspis* occur at very different levels. After all, lithology is the geological expression of the conditions prevailing at the time of deposition and, subject to the limitations of time and space, similar rocks are likely to yield similar fossils: and thus as small a zoological unit as possible, preferably a species, must be used for zonal work. Moreover, in such mixed and variable estuarine and sub-estuarine deposits laid down off a moving shore-line repetitions in lithology are inevitable, for the material is water-sorted into a series of wedge-shaped beds in which the same general succession may often be repeated (cf. Marr, 1929: 78–80, text-fig. 3). And even widely spread deposits, such as the '*Psammosteus*' Limestones (or 'Psammosteid' Limestones, as King called them later), are unlikely in these circumstances to be strictly synchronous. Nevertheless, King's stages provide a most valuable starting-point. His classification for the West Midlands is as follows:

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[1] Read before Section K of the International Geological Congress in London, 1948.

'II. Dittonian. 750–800 ft.	
4. Marls and thin sandstones	200–250′
3. Marls, cornstones, and sandstones	150′
2. Red and green marls and thin sandstones and cornstones	370′
1. *Cephalaspis* sandstone-cornstone	20–30′
'I. Downtonian Marls. 2100–2400 ft.	
10. Marls with purple or green sandstones	100–150′
9. Eurypterid sandstones in red and green marls	90–150′
8. Psammosteid Limestones (1 inch–20 feet) and calcareous sandstones, in green and red marls	70–150′
7. Calcareous light purple and green sandstones, and limy concretions in distinctive bright red and some green marls	180–300′
6. *Ischnacanthus* sandstones and cornstones in red and green marls	90′
5. Deep purple and green marls	400–560′
4. Holdgate coarse sandstone	15–30′
3. Deep purple marls and thin purple sandstones	315–370′
2. *Thyestes* (*Auchenaspis*) or Ledbury marls and sandstones	400′
1. Temeside group (Elles & Slater)	100–200′

'The Ludlow Bone Bed of the Upper Ludlow.'

Two points may be emphasized here: the Ludlow Bone-bed is excluded from the Downtonian, and the whole of the Downtonian and Dittonian series is placed in the Silurian System (King, 1934: 553).

THE SUCCESSION OF FAUNAS

Since the publication of King's paper a very great deal of collecting has been done, adding greatly to our knowledge of the vertebrate faunas, while, so far as possible, previous records have been carefully checked. The following account with the diagram (Fig. 1) summarizes our knowledge of the vertebrate palaeontology of these beds and of the classification which has been based on them as applied in particular to the Shropshire–Herefordshire area (cf. White & Toombs, 1948: 5).

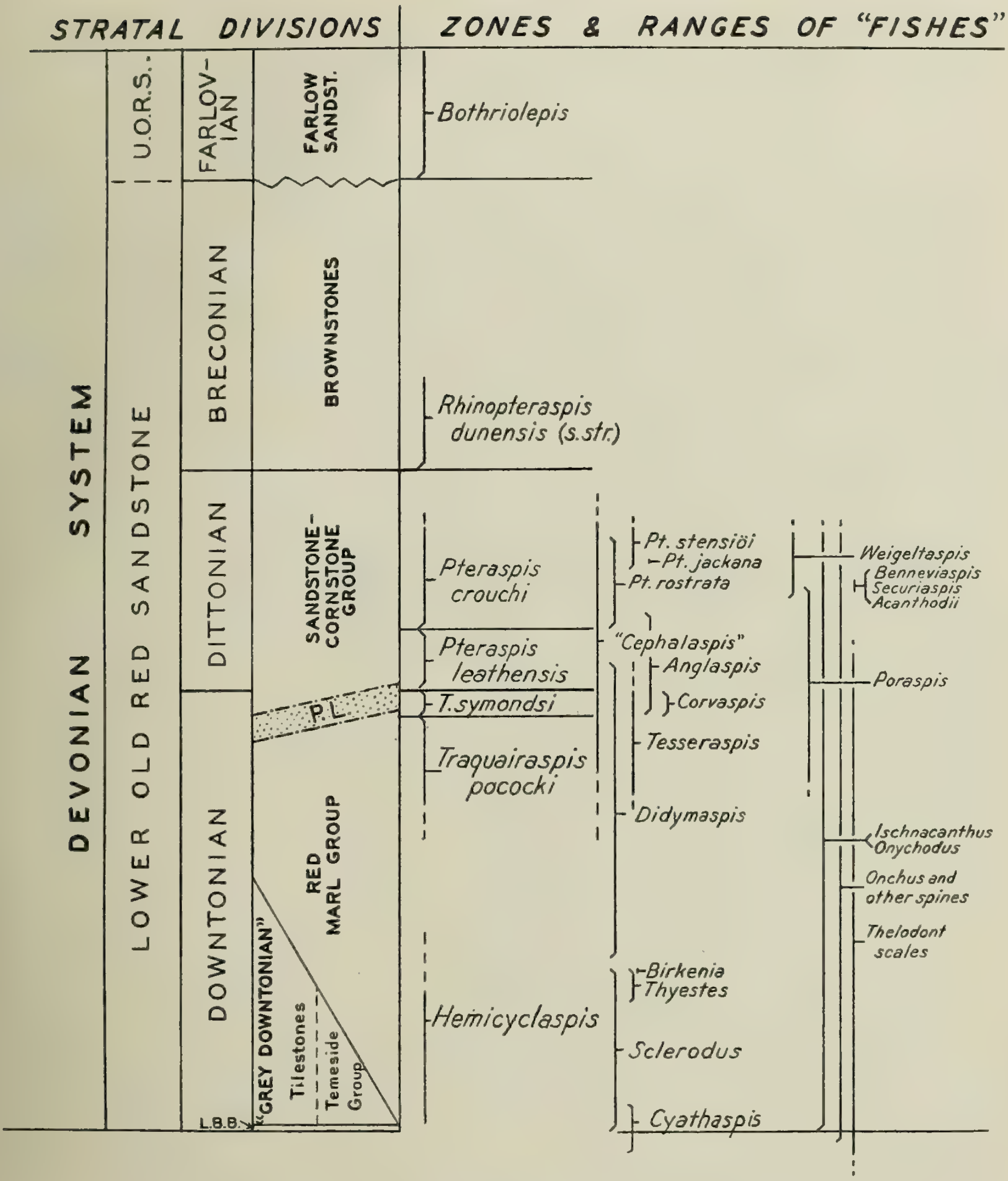
STRATAL DIVISIONS
ZONES & RANGES OF "FISHES"
DEVONIAN SYSTEM
LOWER OLD RED SANDSTONE
U.O.R.S.
FARLOVIAN
FARLOW SANDST.
BRECONIAN
BROWNSTONES
DITTONIAN
SANDSTONE-CORNSTONE GROUP
P.L.
DOWNTONIAN
RED MARL GROUP
"GREY DOWNTONIAN"
Tilestones
Temeside Group
L.B.B.
Bothriolepis
Rhinopteraspis dunensis (s.str.)
Pteraspis crouchi
Pteraspis leathensis
T. symondsi
Traquairaspis pococki
Hemicyclaspis
Pt. stensiöi
Pt. jackana
Pt. rostrata
"Cephalaspis"
Anglaspis
Corvaspis
Tesseraspis
Didymaspis
Birkenia
Thyestes
Sclerodus
Cyathaspis
Weigeltaspis
Benneviaspis
Securiaspis
Acanthodii
Poraspis
Ischnacanthus
Onychodus
Onchus and other spines
Thelodont scales

FIG. 1. Tentative classification of the Old Red Sandstone of the Welsh Borderland. The column is not to scale. [*L.B.B.*, Ludlow Bone-bed; *P.L.*, '*Psammosteus*' Limestones phase.]

The DOWNTONIAN may appropriately start with the LUDLOW BONE-BED, which is only up to 6 in. in thickness. In my opinion there is far more reason from the palaeontological standpoint why this bed should be associated with the succeeding Downtonian strata rather than with the Ludlow Series. The survival in this bed of *Chonetes striatella* and of five other Ludlow species (four brachiopods and a lamellibranch) unknown in the succeeding strata is more than offset by the disappearance of the remainder of the marine fauna. Moreover, although a single specimen of a Cyathaspid (*Archegonaspis*) has been found as early as the Dayia shales (Alexander, 1936: 110) and two specimens of *Cyathaspis* itself[1] with *Thelodus* scales and an *Onchus* spine have been recorded from the Upper Ludlow (Straw, 1927: 88–9), nevertheless this bed is the first horizon which is marked by a definite vertebrate fauna in this region: *Sclerodus pustuliferus* marks the advent of the Cephalaspids in the Anglo-Welsh basin, *Cyathaspis banksi* represents the heterostracans, Thelodont scales the Coelolepids, while ichthyodorulites such as *Onchus* indicate the existence of Acanthodians and perhaps other groups (cf. lists given by Elles & Slater, 1906: 219–20; Stamp, 1923: 396–7).

The TEMESIDE SERIES measures up to some 170 ft. in thickness in the Ludlow district where it forms the so-called 'Grey Downtonian' (Pocock & Whitehead, 1935, 1948, p. 63; see Fig. 2, p. 62 *infra*). It is divided into two zones by Elles & Slater (1906), a lower zone of *Lingula minima* comprising the 'Downton-Castle or Yellow Sandstones', which have yielded *Cyathaspis banksi*, especially plentiful at Bradnor Hill, and an upper zone of *Lingula cornea*, consisting of the 'Temeside or *Eurypterus* Shales'. In the latter occurs the Cephalaspid *Hemicyclaspis*, earlier records of which I have been unable to substantiate. The exact position of the *Thyestes* beds in the zone of *Hemicyclaspis* relative to the Temeside Series is apparently obscured by faulting both at Ludlow and in the famous Ledbury section. In the Ludlow railway cutting, of which no clear or measured section appears to have been published, they seemed to Murchison (1857: 290) to be 'some of the highest beds of the Ludlow Rock' (i.e. Upper Ludlow and Grey Downtonian) almost immediately underlying red marls; in the Ledbury section the *Thyestes* beds are high in the red series, but how high depends on the interpretation of this famous section. Some authors, such as Piper (1898: 313; King MS.), considered that the beds were faulted against the Downton Sandstone, and that most of the Temeside group, lying wholly beneath the red beds (King, 1934: 527), had been cut out. But the evidence is not entirely clear and the succession at Ledbury may be complete (Symonds, 1872: 99), the red rocks being precociously developed and coeval with much of the more typical Grey Downtonian of Ludlow: or to put it another way, the Grey Downtonian is a local development of the RED MARL GROUP, and the level at which the rocks change colour varies with the district. That this is so seems to be supported by the early appearance of the red beds some 50 ft. above the Bone-beds at Brock Hill, Malvern, 4¾ miles to the north-east (Phillips, 1848: 97; Salter, 1858: 10–11).

Purplish marls predominate throughout the RED MARL GROUP and form typically rather featureless country in which exposures are extremely unsatisfactory and fossils correspondingly rare. How far up the *Hemicyclaspis* zone extends is therefore uncertain. The genus is at 450 ft. above the Ludlow Bone-bed in south Staffordshire (King & Lewis, 1917: 94) and more doubtful specimens (P.25387–8) originally recorded as '*Cephalaspis lyellii*' (Marston, 1882: 24) are known from Oakly Park, 2 miles west-north-west of Ludlow, apparently much above the Grey Downtonian.

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[1] Through the courtesy of Dr. R. M. C. Eager I have been able to examine these specimens, of which one, and probably both, is referable to *C. banksi*.

In the upper part of the Red Marl Group reddish and greenish sandstones become prominent and two zones, each characterized by a species of the Ostracoderm genus *Traquairaspis*,[1] may be distinguished. Although the base of the lower zone, that of *T.* [*Phialaspis*] *pococki*, is as yet undetermined, it is interesting to note that near Stonehaven, Kincardineshire, *T. campbelli* which seems closely related to *T. pococki* is associated with a *Hemicyclaspis* that on present evidence is scarcely to be distinguished from *H. murchisoni*. Above the '*pococki*' beds is a zone of *T. symondsi*, maybe up to 150 ft. in thickness. The interesting lithological feature of these upper beds of the Red Marl Group is a phase with characteristic limestones, which vary individually in thickness (1 to 20 ft.) and number. These so-called '*Psammosteus*' Limestones form a marked and valuable feature in the field, noted as long ago as 1870 by M'Cullough (p. 35), for although not necessarily extensive as individual beds, the phase persists over a very wide area from Corvedale to Pembrokeshire and, indeed, has been used by some stratigraphers to separate the Downtonian from the succeeding Dittonian Series (see Fig. 2, opp. p. 62); there is, however, evidence to show that this phase is to some extent diachronic and may occur at levels varying from the top of the *T. pococki* zone, throughout that of *T. symondsi*, and perhaps even into the lower part of the succeeding Dittonian zone of *Pteraspis leathensis*. Since the original distribution of these species was given (White, 1946: 209–14), a number of new records have been added (Hurtle Hill, near Heightington, Worcs.; Mary Moors, near Trimpley; Onen, 5 miles north of west of Monmouth, and several others), from all of which *T. symondsi* has been obtained.

The term '"*Psammosteus*" Limestone' is frequently used in the singular as if only one limestone was present—indeed, it may be, locally, but in general the phrase is misleading, since there may be more than the one.

The difficulty of the fossiliferous levels at Gardener's Bank and Reaside Farm (White, 1946: 209), which are parts of a single long exposure, has now been satisfactorily cleared up by Mr. Toombs, who has shown that the contradictory reports of the position of the fossiliferous layers is due to faulting—in fact the specimens of *T. pococki* lie entirely under the rubbly limestone band, which is some 20 or 30 ft. thick and extends right under the Reaside Farm exposure before fading out, the specimens of *T. symondsi* occurring 10–20 ft. above it, giving a very clear proof of the relationship of the two species.

The vertebrate fauna associated with *T. pococki* consists of *Didymaspis grindrodi* which occurs within a foot or two of *Hemicyclaspis* in south Staffordshire (King &

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[1] The English specimens of this genus were originally referred to *Psammosteus* and later to a new genus *Phialaspis*. New material from Cowie, Stonehaven, has shown that the plates described as *Phialaspis pococki cowiensis* are the ventral disks of *Traquairaspis campbelli*: the generic name must therefore be changed again.

Lewis, 1917: 94), *Tesseraspis tessellata*, *Ischnacanthus*, *Onchus*, *Onychodus*, and *Tolypelepis*, and for the first time in these parts '*Cephalaspis*', i.e. Cephalaspids with cornua other than *Thyestes* or *Sclerodus*.

The '*symondsi*' fauna is similar, but *Corvaspis* has not been found outside this zone and *Anglaspis macculloughi* occurs for the first time. The last named and perhaps *Didymaspis grindrodi* are the only well-defined species that pass up into the zone above, but representatives of the genera *Cephalaspis*, *Onychodus*, and *Thelodus* occur in both zones. *Corvaspis* and *Tesseraspis* have not so far been found in the succeeding zone, but the great change in the vertebrate fauna is the complete replacement of *Traquairaspis* by its distant and more orthodox relative *Pteraspis*. It is, accordingly, here, if anywhere, that a break should be made on palaeontological grounds between the Downtonian and Dittonian.

The lowest DITTONIAN zone is that of *Pteraspis leathensis*, a small blunt-snouted form which has been found in a number of different localities, mostly in the West Midlands, but reaching as far as Brecon (see p. 69 *infra*). The associated vertebrate fauna is relatively large—King (1934: 534) records 'Acanthodian spines' and *Didymaspis grindrodi*, while elsewhere *Poraspis* sp., *Anglaspis ?macculloughi*, *Thelodus* scales (*T.* cf. *schmidti*), Cephalaspid cornua, *Onychodus* teeth, and fragments of an undescribed Ostracoderm or Arthrodire have been found. The beds are chiefly greenish and grey, sometimes purplish sandstones with marls.

The succeeding zone of *Pteraspis crouchi* is considerably thicker, but the top of the range of this species cannot yet be determined, for the sandstones and cornstones, so typical of the lower beds, give way to more marly beds in which there are fewer exposures, and as yet no significant fossils have been found in them. But the lower beds are the most fossiliferous of the whole of the Lower Old Red in this region. The occurrence of the fossils seems highly capricious and local, for the beds are certainly lenticular, soon passing into the more usual barren strata. The dominant fossil is *Pteraspis crouchi*, which is of almost universal occurrence, and then less regular is *P. rostrata*, a variable species which is replaced in one locality by *P. jackana* and towards the top of the zone by *P. stensiöi*. *Securiaspis* and *Benneviaspis* occur rather rarely, but *Cephalaspis* itself is represented by no fewer than sixty 'species', of which less than one-third occurs in more than one locality. Generally the Pteraspids are represented only by isolated plates, usually the dorsal or ventral disks, and the Cephalaspids by head-shields, but in a single small lenticle at Wayne Herbert several complete specimens of *P. rostrata* and of seven species of *Cephalaspis* have been found with Acanthodians, including large Brachyacanthids more than a foot long. A similarly restricted bed at Cwm Mill has also yielded many complete specimens belonging to eight different species of *Cephalaspis*. Other Ostracoderms in this zone are *Poraspis sericea* and *Weigeltaspis*.

In Brecknockshire Mr. W. N. Croft has found in the greenish sandstones of the SENNI BEDS the very long-snouted Coblentzian *Rhinopteraspis dunensis* (s.str.). In Pembrokeshire, at Swanlake Bay (White, 1938: 87), a shorter-snouted form now treated as a separate species, *R. leachi*, occurs in beds reputed to be of lower Dittonian age (Dixon, 1933: 219), but the complexity of the faulting there makes the determination of these beds on stratigraphical grounds somewhat doubtful and, moreover, some of the fossils had been misidentified; therefore in the absence of any other critical information I prefer to regard these beds as of later date.

On the other hand, the reference of the beds near Kidwelly with the primitive *Pteraspis dixoni* (White, 1938: 100) to the Senni Beds on lithological grounds (Dixon, 1904: 37–8; 1939: 229) does suggest that there, at least, beds of Senni type occurred earlier than elsewhere in the Anglo-Welsh area, probably before late Dittonian times (cf. Pringle & George, 1948: 48).

THE ORIGIN OF THE FAUNAS

The interpretation of the conditions under which extinct animals lived and died, especially mobile aquatic animals such as arthropods and fishes, is not easy, but there are certain broad principles by which one may attempt to do so, and by which, briefly argued, I have concluded that the Downtonian and Dittonian vertebrate faunas are in the main spasmodic introductions into the brackish tidal waters from the fresh waters of the mainland (White, 1946: 216), and nothing has since come to light to cause me to modify this view.

With Tertiary and to a less degree with the late Mesozoic fishes one can determine their habitat to some extent by modern analogy, but the farther one goes back the less reliable this becomes and other factors become paramount. With the extinct groups of the Devonian the matter is complicated by the varied conditions then existing; in such an area as the Anglo-Welsh region the faunas may well have been of local brackish-water origin, either alone, or may be mixed with invaders from the truly marine areas or from fresh waters. Gunter (1947) has pointed out that in the modern fauna marine animals, particularly the less specialized forms, are very much more tolerant of lowered salinity than freshwater forms are of increased salinity; the former are therefore more likely to be found in estuarine areas than the latter and, indeed, frequently appear in fresh waters. This, of course, applies to fishes when *alive*; his further deduction that the finding of a fossil fish in a freshwater deposit does not preclude its marine origin, but that its occurrence in a marine deposit makes its marine origin certain must be questioned, for dead and dying fish usually float and in rivers would be swept into the estuaries, so that, in fact, the remains of freshwater fishes are the more likely to occur in estuarine beds. If Gunter's theory held for the Old Red forms, then the marine fauna would be difficult to distinguish from local estuarine species, except possibly by its wider distribution. But whether marine or estuarine, the normal inhabitants of an area would tend to be distributed throughout the rocks rather than to occur as isolated local concentrations, and, apart from local sorting due to winnowing, all parts of the animals would be present even though widely scattered—whether as fragments as in the London Clay or as whole animals as at Monte Bolca depends largely on the circumstances of their death and the rate of deposition. A local fauna destroyed catastrophically, as shown by extreme concentration, would still be detected by its relations to the fauna in the beds below, and possibly above. But the occurrence of the Lower Old Red faunas of the Anglo-Welsh area is peculiar, quite different from those just outlined. The fossils tend to be very localized both geographically and stratigraphically—great thicknesses of rocks seem to be normally barren, and then here and there in the series notable concentrations of Ostracoderms are found. Even where a species occurs throughout a thickness of strata, as do the zone fossils, they tend to occur at definite horizons and with varying associates, e.g. the *Thyestes* accompanying *Hemicyclaspis murchisoni* at Ludlow is *T. salteri*, at Ledbury it is *T. egertoni*, while extreme cases of individuality with very limited lateral distribution are to be found in the fossils of the Dittonian zone of the *Pteraspis crouchi*.[1] The widespread distribution of *Traquairaspis* in the '*Psammosteus*' Limestone phase suggests, like the occurrence of the limestones themselves, conditions of an exceptional kind.

In general these occurrences have the decided appearance of being interpolations derived from a distant source, which is further suggested by the degree, often intense, of water-sorting of the fossils themselves—and, indeed, in the case of the Dittonian deposits by the very different types of sediment in which they are found. These faunules readily call to mind the varied local faunas of complex river-systems, such as are found in South America and Africa to-day, the various branches of which have their own peculiar species of widespread genera and families (e.g. *Barbus*, Cichlids, and Cat-fishes) and all emptying their contents from time to time, by reason of periodic flooding and similar local accidents, into a common basin.

THE SILURIAN–OLD RED BOUNDARY

The vexed question of the Silurian–Old Red boundary has occupied the attention of authors ever since Murchison (1833: 475) first proposed his divisions of the upper part of the 'Grauwacke'. Whether it is really justifiable to endeavour to fix a limit on logical grounds at a single horizon between systems involving thousands of feet of strata may be questioned as straining too far the evidence provided by natural phenomena (cf. Leriche, 1922: 166): after all, the division of the stratigraphical column into systems is entirely a human concept based in detail, at any rate, on local accidents—often only the accident of the particular area where the strata were first studied. Murchison was clearly aware of the difficulties arising from attempting too great precision, and his writings on this subject throughout contain ambiguities and not a few apparent contradictions.

There are several accounts of the history of the Silurian–Old Red boundary question, but some are clearly erroneous and none seems complete; moreover, although one would not necessarily choose the historical division between two systems for modern usage, it is desirable to do so if possible, so that the matter is worth further consideration. In the present instance there has been no little disagreement as to the interpretation of the original author's intentions and the matter is discussed here in some detail.

In his first brief account of the Old Red Sandstone and underlying strata of the Anglo-Welsh basin Murchison (1833) was obviously dealing in very general terms with rocks over a wide area—he remarks (p. 474) on the 'gradual passage from the old red into the grauwacke' but 'however, insists that there are no two formations of the English series which can be better separated from each other for purposes of geological illustration, than the old red sandstone and the uppermost grauwacke; the former being as poor as the latter is rich in organic remains, whilst the colours and mineral characters of the two formations are also very distinct'. Further we read (p. 475) that the Upper Ludlow Rock (the top division of the rocks then generally known as 'grauwacke', underlying 'the base of the old red sandstone') 'is as eminently characterized by the presence of organic remains as the old red sandstone is by their deficiency. Amid a profusion of fossils, the upper beds are characterized throughout the whole range of the formation by two species of Strophomena or Leptæna, an Orbicula, a plicated Terebratula, &c., all of undescribed species'. If one glances at the list of fossils in Elles & Slater's paper (1906: 219–20), it seems clear enough where the 'profusion of fossils', including the brachiopods, stops in the type-area of the Ludlow Series—at the Ludlow Bone-bed: but whether Murchison intended such a definite line of demarcation, or for that matter even knew at this time of the existence of the Ludlow Bone-bed, is most improbable—it was not noted by him until 1839 (p. 198), when it was described as 'the central part of this stratum', i.e. the Upper Ludlow Rock (cf. Murchison, 1854: 137).

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[1] As in four quarries in south-west Herefordshire: Wayne Herbert quarry yields *P. rostrata* with 8 out of 12 Cephalaspids peculiar to it: Castle Mattock *P. crouchi*, *P. jackana*, and *P. stensiöi* with 12 out of 16 Cephalaspids peculiar: Pool Quarry *P. crouchi* and *P. rostrata* with 8 out of 15 Cephalaspids peculiar: Wern Genni *P. crouchi* and *P. stensiöi* with 3 Cephalaspids out of 7 peculiar to it. These quarries lie approximately and respectively at 220, 240, 350, and 650 ft. above the '*Psammosteus*' Limestones.

Murchison's next account (1834*a*, *b*) established the 'Tilestones' as the third and lowest group of the Old Red Sandstone, and where they contain fossils, as in Carmarthenshire and Shropshire they are said to constitute 'the beds of passage into the "*Ludlow Rock*", or highest member of the grauwacke series'. The chart accompanying the paper does not make the line of division any clearer by either the list of fossils or the schedule of localities, but the description of the Tilestones as 'Flaggy, highly micaceous, hard, red and green sandstone' seems to exclude such rocks as the 'Downton-castle building stone', as he later described it (1839: 198), and thus puts the boundary at any rate well above the Ludlow Bone-bed. Certainly, I can see no evidence for the latter part of Dorlodot's (1912: M300) statement that in 1834 the 'Tilestones' division 'Comprend, à sa base, les pierres de construction exploitées près du *Dow(n)ton Castle*'.

In 1835 Murchison first introduced the term 'Silurian System' and contrary to what Stamp (1923: 279) said, made no attempt to define the limits of the system at all, let alone fixing 'the lower limit of the Old Red Sandstone below the Downton Castle Sandstone, i.e. at the horizon of the Ludlow Bone-bed'. It was not until four years later, in *The Silurian System* (1839: 198), that the 'Downton-castle building stone', was named and both it and the Ludlow Bone-bed described; and then, as Jones (1929: 113) has pointed out, Murchison clearly puts the upper limit of his Silurian System at the top of the Downton Sandstone, for he refers (p. 181) to a 'freestone, of which Downton Castle is built, which will presently be described as constituting the upper stratum of the Silurian System'. However, after placing the 'Tilestones' unequivocally in the Old Red Sandstone, the strata between the Old Red Sandstone and the 'true upper Ludlow rock', as the Downton Castle building stone is called (p. 198), are at one and the same time described as 'beds of passage, which cannot be arbitrarily referred either to the Old Red or Silurian Systems', and placed firmly in the 'Upper Ludlow Rock' of the 'Upper Silurian Rocks' (p. 197)! Be that as it may, it seems to me that if any horizon has a right to be considered as the historical dividing line between the two systems, it is that first indicated by Murchison, the top of the 'Downton-castle building stone' as originally defined—that is, the top of bed *Ec* of Elles & Slater (1906: 198) and not the top of their 'Downton Castle or Yellow Sandstones', which comprise very much more than Murchison's 'building stone', being 30–40 ft. thick against the latter's 12–14 ft.

Later, of course, Murchison (1845; 485) transferred the Tilestones to the Silurian System on palaeontological grounds under, as Dorlodot (1912: M302) and Straw (1930: 95) have suggested, the misguided influence of faunal lists in which fossils from older rocks are included under the heading of 'Tilestones'. Murchison later admitted (1859: 149) that the fossils were obtained from 'Clun Forest and some parts of S. Wales, where the bone-bed has not yet been seen'—that is, from areas where the typical Ludlow sequence is not developed and where stratal boundaries are least clearly marked.

It is evident that Murchison never used the Ludlow Bone-bed as a boundary between stratal divisions, either major or minor, and Dorlodot's assertion (1912: M303, M366) that Murchison in 1842 (p. 648) considered the Ludlow Bone-bed to mark the top of the Silurian System is based on the misunderstanding of a piece of rhetoric removed from its context. Probably its first use as a boundary between the two systems may be attributed to Page (1859: 93).

After Murchison's work the next important development was the establishment by Lapworth (1879–80) of the Downtonian, composed of the Downton Sandstone (*s.s.*), Bone Beds (presumably Murchison's 'Fish Beds'), and the Upper Ludlow (erroneously printed in the table as 'Lower Ludlow'). It is therefore the exact equivalent of Murchison's 'true Upper Ludlow rock' (1839: 198–201). This term 'Downtonian' soon seems to have been abandoned by Lapworth (1888: 172), but it was later adopted by Peach & Horne (1899: 568) for beds supposed to correspond to Geikie's (1893: 753) top division of his Ludlow Group (consisting of 'Tilestones, Downton Castle Stone and Ledbury Shales') in the Lanarkshire and Ayrshire succession, comprising some 2,800 ft. of strata. This meant that in the Anglo-Welsh area of Lapworth's original 'Downtonian' only the 14 ft. of the original 'Downton-castle building stone' and a few feet of the 'Bone Beds' was left, the Tilestones and Passage beds being added above and the Upper Ludlow removed from below (Fig. 2).

Elles & Slater (1906) used the Ludlow Bone-bed as the upper boundary of their Upper Ludlow Group, thus dividing it from their 'Temeside Group', which for them formed the top of the Silurian System; but the real stratigraphical significance of this bed seems first to have been realized on the other side of the Channel, first by Dorlodot (1912) and then by Barrois, Pruvost, & Dubois (1918: 710; 1922: 225), who made it the base of the whole Devonian System—a suggestion which was readily accepted and elaborated by Stamp (1920; 1923).

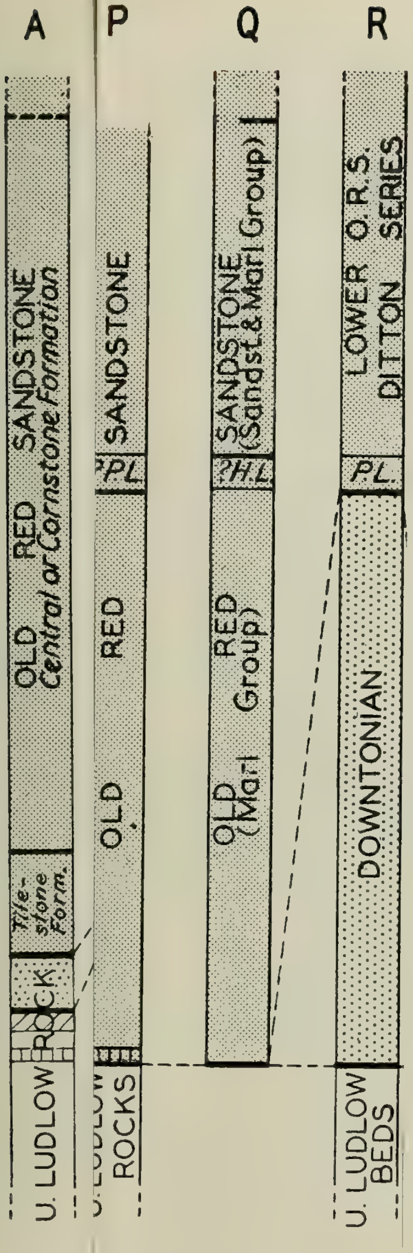
It is all the more unfortunate that these distinguished French authors have misunderstood Murchison's original statements regarding the boundary, and have in consequence put forward as further support for their otherwise admirable arguments historical evidence that is certainly erroneous. It is just not true, as Barrois, Pruvost, & Dubois have stated (1922: 214), that the upper limit of the Silurian System 'a été fixée d'abord, en 1838, par cet auteur (Murchison 1839), entre l'Upper Ludlow Rock et les Tilestones (grès de Downton) . . .' and then 'au Ludlow bone bed (sommet de l'Upper Ludlow Rock)'. One need only comment that in *The Silurian System* (*a*) the Downton Castle building stone is clearly placed in the Upper Ludlow Rock and not in the Tilestones (p. 198); (*b*) the upper limit of the Silurian System is placed at the top of the 'building stone' and not at its bottom (p. 181); and (*c*), as noted above, the Ludlow Bone-bed (a name which, incidentally, Murchison does not seem to have used until 1854, caption p. 143) is described as 'the central part of this stratum', i.e. of the Upper Ludlow Rock (p. 198), and not the top, and he seems never to have altered his opinion (1872: 133). As Jones (1929: 115) has pointed out, Geikie (1882: 682; 1903: 961) appears to have been the first to have misinterpreted Murchison who, he says, originally called the Downton Sandstone and 'the whole of these flaggy upper parts of the Ludlow group' Tilestones. What Murchison did do in *Siluria* (1854: 139) was to include his 'Downton Castle building stones' with the Tilestones in his 'band of transition', which is quite another matter, and we may note that by this time the Tilestones themselves had been removed to the Silurian System. Much of the difficulty may be traced to the varied use by Murchison of such terms as 'beds of passage', 'transition beds', and 'tilestones', e.g. in 1834: 12 we read 'these fossiliferous tilestones constitute the beds of passage into the "*Ludlow Rock*" ', whereas in 1839: 197 'tilestones' are in the Old Red Sandstone, but the 'beds of passage' are something lower, 'which cannot be arbitrarily referred either to the Old Red or Silurian Systems'.

In the meantime King & Lewis (1917) had initiated a most important innovation in respect of the Anglo-Welsh area of extending the Downtonian upwards to include some hundreds of feet of the overlying red beds, later (King, 1921*a*; 1925; 1934) to be increased to over 2,000 ft. of rocks, while a further 800 ft., all the strata previously referred to the Lower Old Red which were supposed to contain *Pteraspis crouchi* and *P. rostrata*, were placed in a new series, the Dittonian, and on the alleged grounds of faunal continuity both Downtonian and Dittonian were classed as Silurian.

Up to this point, the controversy regarding the boundary in the Welsh Border region had concerned only some 200 ft. of strata at the base, i.e. the beds between the Ludlow Bone-bed and the top of the Passage Beds; but Wickham King's ideas involved the almost complete annihilation of the Lower Old Red in the Anglo-Welsh region. So far King has not been largely supported in this revolutionary classification, but we may note Dahmer's (1948) provisional statement, based on the study of Mollusca, Ostracods, &c., that 'Alle Ablagerungen, die bisher unter der Bezeichnung "Gedinne" in der Literatur geführt und an die Basis des Devons gestellt wurden, haben Ludlow-Alter.' Allan (1935: 39) certainly fixed the Siluro-Devonian boundary 'to agree with the incoming in force of the faunas associated with the *cyclopterus-hystericus* type of *Spirifer*', that is, at the base of the Taunusian or Lower Siegenian in western Europe; but that author admits that this limit is artificial, since 'a complete succession of strata with marine faunas of the open-water type' exists in north-east America and 'where the facies is stable, therefore, there is no faunal break between the Silurian and the Devonian', and the value of this effort to establish a universal boundary is somewhat abated by his subsequent discovery (Allan, 1947: 451) that 'the similarity between the New Zealand fauna and that of Western Europe was to a large extent superficial and that many of the apparent similarities were based on comparison of homeomorphous groups'. Other authors have produced a remarkable number of varied classifications within recent years, as the accompanying Fig. 2 shows, and although in no case is the Dittonian included in the Silurian System, the position of the Downtonian still seems unsettled, some placing it in the Old Red, others in the Silurian, while still others leave the question open.

Obviously, such differences of opinion, and especially in the type-area, can only lead to further confusion both here and elsewhere, and therefore the arrangement here described, based on the more recent information regarding the vertebrate succession, is put forward only in the hope that it may help towards stability. In my opinion there is, as Wickham King suggests, a general faunal continuity throughout the Downtonian–Dittonian strata as illustrated by the first diagram, but I differ from him in considering that, so far as the Anglo-Welsh cuvette is concerned, the demands of both stratigraphy and palaeontology are best met by retaining the whole in the Lower Old Red Sandstone. The complaint of some writers that the break at the Ludlow Bone-bed does not provide a valid reason for placing the boundary there since the change in fauna is due to a change in facies (Leriche, 1922; Evans in Stamp, 1921: 8; in Stamp, 1923: 277; Allan, 1935: 46) does not seem to me to be wholly justified. The arguments in favour of using a marine succession as the standard in matters of stratigraphical definition were clearly stated many years ago by Blanford (1885: 706–11). In some ways the use of a marine succession is obviously preferable, particularly in that sea-faunas may move rapidly over wide areas, but the arguments are by no means all one-sided and some put forward seem rather two-edged—for instance, Elles's (1924: 87) contention 'that the faunas of the deeper-water areas where conditions are more uniform should furnish the standard for purposes of classification' is largely countered, quite unwittingly, by Allan's previously quoted remark (1935: 59) that 'where the facies is stable, therefore, there is no faunal break between the Silurian and the Devonian', and by his consequent selection of an artificial limit between them. Moreover, Miss Elles's further claim that under constant physical conditions any change in the character of the fauna 'is almost bound to be of real significance' is open to considerable doubt. If conditions were ideally uniform over a long period one might be able to detect in the fossil assemblages indications of varying rates of evolution in species or even larger groups of organisms (cf. Simpson, 1944: 48, &c.), but the general aspect of the fauna would be unlikely to show a discernible break at any one point; indeed, one would at once suspect that a faunal change in apparently continuous strata was due to a change in conditions, such as an increase or decrease in temperature or salinity, not reflected in the lithology. Allan's criticism (1935: 47) that 'it is inconceivable that an international classification can be based on the fish-faunas, which are, practically speaking, confined to a single facies in Western Europe', cannot be accepted, for to ignore the 'fish-faunas' in order to fix an admittedly artificial limit outside the original area based on another set of organisms seems unreasonable, and, as it turned out, not particularly fortunate (Allan, 1947: 451).

Leriche (1922: 164) has objected to Stamp's rather extravagant statement (1922: 91) that 'Le commencement du Dévonien correspond donc à l'aurore d'un âge de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OLD RED SANDSTONE
Central or Cornstone Formation
Tile-stone Form.
ROCK
U. LUDLOW
OLD RED SANDSTONE
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LUDLOW
ROCKS
OLD RED SANDSTONE
(Marl Group)
(Sandst. & Marl Group)
?H.L
LOWER O.R.S.
DITTON SERIES
PL.
DOWNTONIAN
U. LUDLOW BEDS

d Dittonian strata in the Ang
ses based on King 1934, but

l 1948: 63, 65.
d 1948, fig. 34.
7.

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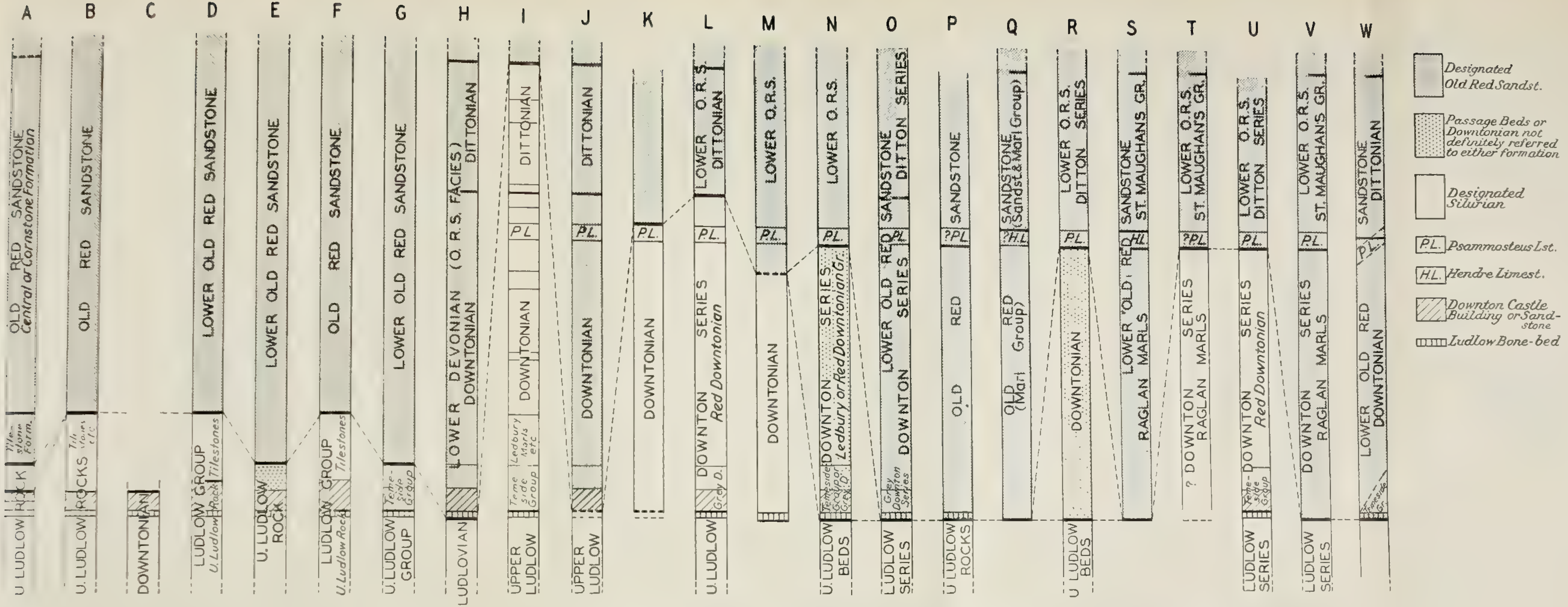
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Designated Old Red Sandst.
Passage Beds or Downtonian not definitely referred to either formation
Designated Silurian
P.L. Psammosteus Lst.
H.L. Hendre Limest.
Downton Castle Building or Sandstone
Ludlow Bone-bed

FIG. 2. Diagram illustrating variations in level of the Silurian–Old Red boundary and in the classification of the Downtonian and Dittonian strata in the Anglo-Welsh area published by field-workers since 1920 compared with the classifications of Murchison, Lapworth, Geikie, and Elles & Slater. (Comparative thicknesses based on King 1934, but thinner divisions much exaggerated.)

A. Murchison, 1839: 197–8
B. Murchison, 1854: 138–9 (also 1872: 134–5).
C. Lapworth, 1879–80
D. Geikie, 1882: 674, 681–2
E. Lapworth, 1888: 173, 180
F. Geikie, 1903: 953, 960–1.
G. Elles & Slater, 1906
H. Stamp, 1920, 1923: 277
I. King, 1921, 1925, 1934
J. Richardson, 1935: 3
K. Practice of the Geological Survey in Richardson, 1935: 3, footnote
L. Pocock & Whitehead, 1935 and 1948: 63–65
M. Pocock & Whitehead, 1935 and 1948, fig. 34
N. Edmunds & Oakley, 1935, 1947
O. Pringle & George, 1937, 1948.
P. Rose, 1937: 58.
Q. Dunham, 1937–8.
R. Dunham, 1936: 34
S. Pocock, 1940: 25
T. Trotter, 1942: 9
U. Whitehead & Pocock, 1947: 4–11.
V. Kellaway & Welch, 1948: 15.
W. Modified after White & Toombs, 1948.

vertébrés'—there were, of course, vertebrates long before those times—but if we consider the statement in a restricted geographical sense, it is true that in the Anglo-Welsh cuvette the remains of vertebrates appear as common and obvious fossils for the first time in the Ludlow Bone-bed.

Objections of some sort or another may, indeed, be raised to any division of strata based on palaeontological grounds—obviously, since life is continuous (or unless one believes in Special Creation), somewhere or other there are in strata coeval with the Silurian Upper Ludlow faunas immediately ancestral and perhaps hardly to be distinguished from, the Downtonian faunas, although they may never be brought to light. Faunas may vanish suddenly and finally (although such complete disappearances are probably rare in nature), but sudden appearances can only be local. Our choice of limits must therefore be to some extent arbitrary, and in disputed cases (which means in most cases) be subject to some agreed convention, of which the most obvious is a law of priority—that is to say, the division must be based on a standard succession which should be in the area first described and that the limit should approximate to that originally designated, having regard to the demands of practicability. In the case of the Silurian–Old Red boundary, the type-area is our Ludlow area and the originally defined boundary was the top of the 'Downton Castle building stone' of Murchison (1839: 198—bed *Ec* of Elles & Slater, 1906). In this instance the demands of practicability do require some slight adjustment, for this is not a level of any marked faunal change nor is it lithologically easily recognizable very far away from the immediate neighbourhood of Ludlow, so that one may consider, as other authors for a variety of reasons have already done, the claims of the Ludlow Bone-bed, only a matter of 15 ft. below in the typical Downton Castle area (Elles & Slater, 1906: 213, fig. 6). It is in this conspicuous and widely spread stratum that the incoming of the vertebrate faunas in the type area is most marked and corresponding changes have been noted in respect of the invertebrates and in the lithology at comparable levels in less typical areas of the cuvette (e.g. Straw, 1930: 95, 100; Earp, 1938: 150). Farther afield, satisfactorily close correlation between the type section and the more mixed successions should be possible when the faunas have been reconsidered in detail and through them with the more completely marine areas. As matters now stand the marine faunas are not well enough known (cf. Shirley, 1938; Dahmer, 1948) for their claims to be pressed against those of the continental faunas with their historical background in determining the uppermost limit of the Silurian System: indeed, there is likelihood of confusion were this done. It is essential that the boundary be fixed now and, in my opinion, the Ludlow Bone-bed provides by far the most satisfactory datum line from which to mark the boundary in other areas. This line has already been strongly advocated on the Continent, as we have previously noted.

In the mixed succession around Liévin, in north France, attempts have been made to correlate the beds with the Shropshire succession, but that the sections there reach so far down as the level of the base of our Downtonian is not now considered likely (Shirley, 1938). Barrois, Pruvost, & Dubois (1922: 180–4, &c.) believed that change from Silurian to Marine Devonian faunas took place a little before the onset of Old Red conditions, which first show themselves at the boundary between the

'Schistes de Méricourt' and the 'Psammites de Liévin', where alternations of marine and continental deposits are present.

The Psammites are interesting in that they have yielded a small *Poraspis*, *P. barroisi* and, more important, a small blunt-snouted *Pteraspis*, *P. gosseleti* (see Leriche, 1906), which is exceedingly close to *P. leathensis*, and I have no hesitation in suggesting the correlation of the 'Psammites' with the *leathensis* beds of our area.

This implies that the '*leathensis*' beds are of upper Lower Gedinnian age (Barrois, Pruvost, & Dubois, 1922: pl. vii) and that therefore the whole of the Downtonian, over 2,000 ft., must be equivalent to the marine 'Schistes de Méricourt', which are only up to 120 ft. thick; but Shirley (1938: 358) after reconsidering the marine faunas there suggests that the whole of the succession preserved, some 300–400 ft. of rocks, is probably post-Ludlow in age, the top of the Silurian being absent.

Thereafter, in France and Belgium (see Asselberghs, 1946) as over here[1] there follow beds with *Pteraspis crouchi* and *rostrata*, to be correlated with the Upper Gedinnian, and finally there are the Siegenian and Emsian beds with *R. dunensis*. Thus in general the successions on the Continent and in the Anglo-Welsh area show considerable resemblance to one another.

Säve-Söderbergh (1941) made a brief but comprehensive survey of the Downtonian-Dittonian rocks elsewhere and with his conclusions I find little to disagree—he does, I think, over-emphasize the importance of the faunal break between the two series at King's level, i.e. between the *leathensis* and *crouchi* beds—the more important break is certainly lower down, below the *leathensis* zone. He concludes that the Norwegian *Hemicyclaspis* fauna is early Downtonian, and correlates the Oesel main fish-bed with the Lower Ludlow—this, we may note again, contains a Cephalaspid referred to the genus *Thyestes*, and another identified as *Cephalaspis* itself.

The Spitsbergen faunas were also dealt with by Føyn & Heintz (1943: 42), who consider that the lower part of the Red Bay Series, the Fraenkelryggen Division, is of upper Downtonian age (i.e. lower Dittonian according to our classification), since it contains, besides numerous small forms of *Poraspis* and *Cephalaspis*, species of *Anglaspis* and a blunt-snouted *Pteraspis*, *P. primaeva*, possibly related to *P. leathensis* and at its base *Phialaspis* (*Traquairaspis*) and *Corvaspis*; while the succeeding Ben Nevis Division, with numerous Cephalaspids including *Benneviaspis*, is regarded as Dittonian in age. Säve-Söderbergh suggested that the Downtonian–Dittonian boundary (of King) may be some way down the Fraenkelryggen Division, and although our knowledge of neither the English nor the Spitsbergen faunas is yet sufficiently complete to justify more than broad generalizations, our present information regarding the Anglo-Welsh faunas suggests that only the base of the Fraenkelryggen Division should be considered to be Downtonian.

In conclusion, I would like to express my warmest thanks to those who have given me, as usual, every help in compiling these notes—Mr. Wickham King, ever generous with information and advice; Dr. R. W. Pocock, Professor L. J. Wills, and Mr. H. A. Toombs, without whose help in the field and laboratory much of this could not have been written; and Mr. F. M. Wonnacott, who prepared the bibliography.

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[1] The significance of the '*dewalquei*' fauna is uncertain, as the identity of that species, which has been referred to *R. dunensis*, is not clear. The association of *R. dunensis* with *P. rostrata* in the Grès de Vimy, based on specimens referred to *P. dewalquei*, is disputed (Asselberghs, 1943: B38 footnote), while the occurrence of *R. dunensis* in the 'carrière de l'Albaule' in beds supposedly equivalent to '*crouchi*' beds (Asselberghs, 1943) is not proven. Professor Asselberghs informs me that nowhere have *R. dunensis* and *P. crouchi* or *P. rostrata* been found directly associated.

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PTERASPIS LEATHENSIS WHITE
A DITTONIAN ZONE-FOSSIL

By ERROL IVOR WHITE

SYNOPSIS

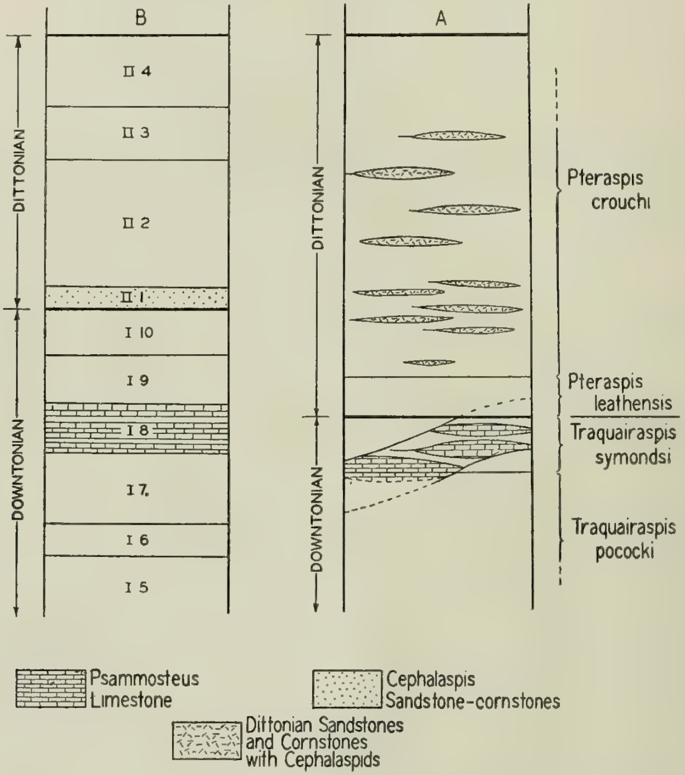
The Lower Old Red Sandstone species *Pteraspis leathensis* White, from the Anglo-Welsh area, is described in detail and compared with Continental species with which it is considered to form a new sub-genus, *Simopteraspis*. Its use as a zone-fossil in the Dittonian is demonstrated.

I. INTRODUCTION

Pteraspis leathensis is the earliest species of this genus recorded from Great Britain and is of special interest on that account alone. Moreover, although published records name only five localities from which it has been obtained (King, 1934: 534, 541; White, 1935, text-figs. 30, 31, 38, and 77), subsequent discoveries have shown that this species has apparently a wide geographical distribution, at least within the Anglo-Welsh area, and a limited stratigraphical range within the Lower Old Red Sandstone, so that its value as a potential zone-fossil in this intractable series is obvious. Indeed, not only has it already been used as such (White & Toombs, 1948), but the zone, which follows immediately that of *Traquairaspis* [*Phialaspis*] *symondsi*, is taken as the revised base of the Dittonian Series (Text-fig. 1), since it is here rather than later, as originally put forward by Wickham King (1925, 1934), that a significant change takes place in the vertebrate faunas of the Lower Old Red (p. 56 *supra*). The species was not described until 1934, but it had been recorded by King in 1921 (as *Cyathaspis leathensis*), and later (1925: 387) again without locality, as occurring 'in or near the *Psammosteus* Limestones', which is approximately correct, although these beds were reckoned as Downtonian by King, who placed the base of the Dittonian considerably higher, within our zone of *Pteraspis crouchi*. The first locality actually mentioned by King (1934: 534) was Ammons Hill; at the same time he extended the range of the species upwards into his Dittonian (ibid.: 446), but no confirmation of this has been forthcoming, and it seems likely that this suggestion was based on the mistaken identification of plates of juvenile specimens of *P. crouchi* or some other species. It is surely significant that in none of the numerous localities from which *P. leathensis* has been obtained have specimens of the other species of *Pteraspis*, typical of the succeeding zones, been found, and in the only two areas from which both *P. leathensis* and the earlier zone-fossil *Traquairaspis symondsi* have been collected, in Lye Stream (loc. 7*b*) and near Brecon (8), the two zones are clearly distinguished.

Whether the '*Psammosteus* Limestones' phase does actually invade the zone of *P. leathensis* (or, to put it the other way, as Wickham King has reported, whether *P. leathensis* occurs in the *Psammosteus* Limestones) is not yet clear (see Lye Stream section, p. 74 *infra*), but since that phase is almost certainly diachronic, it seems possible that it does.

Outside the Anglo-Welsh area closely related species have been found in north France and Spitsbergen, in the former the resemblance being so close as to suggest possible identity when the French fossils are better known.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Pteraspis crouchi
Pteraspis leathensis
Traquairaspis symondsi
Traquairaspis pococki
Psammosteus Limestone
Cephalaspis Sandstone-cornstones
Dittonian Sandstones and Cornstones with Cephalaspids

TEXT-FIG. 1. Diagrammatic representation of the classification of the Dittonian and upper Downtonian strata of the Anglo-Welsh region used in this work (A) compared with that of Wickham King, 1934, (B) to show the diachronic nature of the '*Psammosteus* Limestones' and the general distribution of sandstones and cornstones with Cephalaspids for comparison with the supposed '*Cephalaspis* Sandstone-Cornstones' of King.

II. THE LOCALITIES AND ASSOCIATED FOSSILS

1. *Leath 1 (or Leath Stream), Corvedale, Salop.*

'Leath Stream (1) is a rivulet on N. side of the road at Leath Bank, the steep hill on road from Ditton Priors to Holdgate and Stanton Long. There is one cottage on the side of this road at Leath Bank and the section (in rivulet) is a little to E. of this cottage. This is I. 8 but it is high up in this stage as the hard band (in I. 8 base at Earnstrey [slightly less than a mile away to the SW.]) crosses Leath Bank below and W. of the cottage and its garden on that bank—all specimens [from] Leath Stream (1) I. 8 are out of this rivulet E. of this cottage.' (W. W. King *in lit.*

16 June 1945.) Some of the specimens are labelled 'Lower band' or 'Lowest band'.

This is the type-locality. The specimens include the holotype, the external impression of an almost whole but completely flattened dorsal shield, and about a dozen other specimens, mostly ventral disks, but including one deep flank-scale (B.U.11[1]), a fine dorsal spine and socket (P.14522), and an impression of the left antero-lateral region of a dorsal shield (P.16853*ii*). The specimens are shown either from the inner side (now often developed as external impressions) or the outer surface, and although usually crushed the preservation of the external ornamentation is very fine. The fossils are black in a matrix of light grey muddy limestone with much carbonaceous material on the exposed surface and some *Pachytheca*. No other fossils have been obtained.

2. *Ammons Hill, Bromyard, Herefordshire*

The section is in the railway cutting between Suckley and Bromyard stations on the B.R.(W.R.); it is described in some detail by Wickham King (1934: 533–4) who records all his stages from I. 7 to II. 2, of which stages I. 7 (part) to I. 10 comprise some 440 ft. of strata. This might be expected to cover approximately the Downtonian zones of *Traquairaspis pococki*, *T. symondsi*, the Dittonian zone of *Pteraspis leathensis*, and part of that of *P. crouchi*, but the section is now much overgrown and of these zone-fossils only *P. leathensis* has been collected. Wickham King records specimens only from his stage I. 9 (according to his unpublished section from bed '11' in the middle of the stage) in 'dark green, very fine silts and marls', with *Didymaspis grindrodi*, 'Acanthodian spines' (these specimens have not been traced), mollusca, eurypterids, and *Pachytheca*, but a ventral disk collected by him (P.16537–8) is labelled 'top part of I. 8'. The specimens described below, chiefly collected by Messrs. W. N. Croft and R. P. Tripp, are in a fine red sandstone, sometimes mottled green and somewhat calcareous, which apparently lies immediately over King's bed '11' and at least 140 ft. above the 'Psammosteid Limestone' marked at the base of stage I. 8 in King's measured section of the cutting. *P. leathensis* seems, therefore, to have been collected at more than one level. The fauna associated with the red sandstone specimens, which include the uncrushed external impressions of one complete and several fragments of dorsal shields and of a number of isolated ventral disks (Text-figs. 3–5, 9), comprises an *Onychodus* spiral (P.23746) and other undetermined plates and spines.

3. *Dinmore Hill, Herefordshire*

Dinmore Hill is 7½ miles north of Hereford. W. S. Symonds (1872: 222) remarks that 'Fish plates were found in the tunnel [i.e. the railway tunnel through the hill], but I saw nothing new or worthy of remark'. A single small and imperfect ventral disk in counterpart with ornamentation typical of *P. leathensis* (P.16543–4) was collected by Mr. Wickham King 'by tunnel shaft, near top of ridge near road to Leominster, I. 8'.

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[1] Specimens lettered 'B.U.' belong to the Geological Department of Birmingham University; 'RP' and 'De' to H.M. Geological Survey; 'P.' to the British Museum (Natural History).

4. *Porch Brook, Rock, Worcestershire*

R. W. Pocock, who discovered this fossiliferous locality, described the exposure as '*Anglaspis* Bed (Top Bed) 550 yds. S. of Whitehouse Farm. In Porch Brook'. L. J. Wills's exposure, from which came most of the specimens considered here, is described as '500 yds. S. by W. of White House Farm $\frac{3}{4}$ (mile) SE. of Rock near Bewdley'. According to Wickham King the stage is I. 8 (*in lit.* 20 June 1945).

The rock is a light grey calcareous siltstone on which the remains of the Ostracoderms, black in colour, are freely scattered (Text-figs. 6–8, 10–14; Pl. 5, Figs. 1–5). The specimens are mostly quite small fragments and scales but include a few large pieces of dorsal shields. Identifiable remains of ventral disks are rare. Curiously enough, while the shields are very much smaller than those from other localities the scales are relatively very large. Most of the fossils show their outer surfaces, which are very well preserved.

Besides the remains of the *Pteraspis*, which constitute the bulk of the material, pieces of *Anglaspis* (e.g. P.25250), presumably *A. macculloughi*, are numerous, with scales of a *Thelodus* (*T.* cf. *schmidti*) (e.g. RP695), a few fragments of ichthyodorulites, and scales and fragments of plates of one or more undescribed Ostracoderms with characteristic ornamentation. The underside of the slabs, that is to say, about an inch above or below the Ostracoderms, there is much carbonaceous material, with an occasional *Pachytheca* and more rarely pieces of the Ostracoderms poorly preserved.

5. *Holbeache, Trimpley, Worcestershire*

A single specimen labelled 'Holbeache 6' was collected by Wickham King from an exposure in the plantation, rather more than 100 yds. north-east of Holbeache House, 'by the cart track to Payne's Cottage'. In this track Roberts (1860: 104) was able to 'knock out a *Pteraspis*', presumably from the same bed. This is about a furlong from the spot where *Traquairaspis* [*Phialaspis*] *symondsi* was found (White, 1946: 211). Unfortunately the relative levels of the two finds have not been clearly determined.

The specimen (P.24791) consists of a crushed ventral disk showing the outer surface overlying an inverted dorsal disk with a branchial plate at the side—probably the remains of a single carapace. Another fragment lies near by. The specimens are black on a gritty greenish cornstone with yellow pellets.

6. '*Near Trimpley*', *Worcestershire*

The exact provenance of these three ventral disks is unknown. The matrix is a fine-grained, light grey sandstone, and the one actual plate (now etched to form an external impression, B.M. (N.H.) 42159*a*) was similar in colour. The other specimens are internal impressions (42159, the counterpart of the plate previously mentioned, 42160, 42160*a*—see White, 1935, text-figs. 38, 77) of medium size, measuring 3·5–3·7 cm. in length. They are almost undistorted, and show well the shape and curvature of the plates. Recently a fourth specimen, 42160*b*, the internal impression of a dorsal shield as small as the Porch Brook specimens, has come to hand. Its matrix is similar to but rather bluer than that of the ventral disks and it is simply labelled

'Trimpley'. All these specimens are from the Baugh Collection and were discovered before 1870.

7. *Exposures near Morville, Salop.*

To the south and south-west of Morville, 3 miles west of Bridgnorth, seven localities have yielded small vertebrate faunas with *Pteraspis leathensis*. Six of these were discovered during the 1929 survey of the area, and in the Summary of Progress of the Geological Survey for 1929 (p. 50) it is stated that 'Fish beds, probably belonging to the Lower Old Red Sandstone (Dittonian), have been detected by Mr. Pocock in the sandstones and marls above the *Psammosteus* Limestone of Meadowley Hill, and at localities in the area to the south-west round Criddon and Chetton'. More details are given in the recent memoir (Whitehead & Pocock, 1947: 22).

Three of the Survey exposures (*c*, *d*, *g*) were loose blocks, but those clearly in place (*a*, *e*, *f*) were above the '*Psammosteus* Limestones' according to the Survey mapping. Mr. Wickham King's manuscript maps agree with this except in respect of Yewtree Dingle (*e*), where he places the '*leathensis*' exposure just below the '*Psammosteus* Limestones'. Both these conflicting statements may well be true, for the '*Psammosteus* Limestones' stage (I. 8) as defined by King (1934: 527) is up to 150 ft. thick and may contain more than one limestone (see Text-fig. 1). It was originally designated a zone, but recent work (White & Toombs, 1948: 7) indicates that it was a diachronic phase which occurred in at least two zones (*Traquairaspis pococki* and *T. symondsi*) and possibly still higher in that of *Pteraspis leathensis*, a suggestion which may explain the above apparent contradiction. Indeed, it was at first thought that in the Lye Stream section (*b*) full proof was forthcoming, since beds containing *P. leathensis* have been found both above and below the representative of the limestone phase, but later investigations throw much doubt as to the lower bed being in place, a doubt which also applies to the finds at some of the other localities (e.g. (*c*), (*d*), and (*g*)), all of which except (*a*) lie on the arc of the Meadowley–Aston Hill ridge within a distance of ¾ mile.

The matrices are for the most part grey sandstones or marls, occasionally cornstones with variable lime-content. The fossils, which are also light in colour, are often fragmentary, but do include some fairly complete dorsal and ventral disks on which the ornamentation is well preserved, and there are also a number of good internal casts.

Wills (1948: 28 footnote) records a small slab from Morville with 3 ventral and 30 dorsal disks, of which 'all but four lie upside down, as if the animals in dying had turned turtle and had then been stranded on their backs on the muddy bottom of a pool. Presumably as decomposition set in, the other parts of the skeleton were drifted away by currents.' This is a singular explanation of an effect of water-sorting. Quite apart from the unlikelihood of mud being left behind by a current that could carry away the ventral disks and branchial plates, we would suggest that saucer- or cup-shaped objects, unless subjected to violent movement, tend to sink in water with the convex surface downwards, since that surface presents less resistance than the concave side to passage through the water (the same, of course, applies reversely to objects rising in air). On the other hand, if the plates had been further subjected to stream-pressure after settling, they would presumably have followed the example of Richter's pelecypod valves (Arkell, 1943: 147) and have come to rest with the convex surface upwards. Current- or water-sorting is commonly met with in the Lower Old Red sandstones (see White, 1938: 110; 1946: 215) and in some cases not only are the types of plates segregated, but the plates are more or less uniformly orientated. The determining factor in water-sorting is not size, as Wills suggests, but buoyancy, depending on shape and specific gravity, e.g. it is often the case that the domed dorsal and the flat ventral disks of *Traquairaspis*, of approximately the same size, are found in separate localities.

The localities are as follows, the details, except in the case of (*b*), being those given on the labels of specimens in the Geological Survey, most of which were collected by or at the instance of Dr. Pocock:

(*a*) Section in south bank of brook, 930 yds. S. 5° W. of Meadowley Farm, and 2,490 yds. S. 9° W. of Morville Church. [Also given as 'Stream bank section 700 yds. NE. of Criddon Farm near Chetton' and in Whitehead & Pocock, 1947: 22, as '700 yds. upstream from Criddon Bridge'.]

Associated with the *Pteraspis* plates (e.g. De3881–7, RP331) are scales of *Thelodus* cf. *schmidti* (e.g. De3884), fragments of an undescribed Ostracoderm or Arthrodire (De3883*a*) and *Pachytheca*.

(*b*) The Lye Stream, 490 yds. W. 17° S. to 800 yds. W. 23° S. of Lye Bridge. This is a most important section, for it exposes some 150 ft. of roughly horizontal strata, and clearly establishes not only the relationships between the *Traquairaspis symondsi* fauna and that of *P. leathensis*, but also the diachronism of the '*Psammosteus* Limestones', since it is only here and elsewhere in this area that they are found above *T. symondsi*. Mr. H. A. Toombs, who made a detailed study of the section, found towards the base, at about 370 ft. O.D., a hitherto unrecorded bed with *Traquairaspis symondsi*, in which the zone-fossil was well and plentifully preserved. Some 60 ft. above this were blocks in the bed of the stream, containing plates of *P. leathensis* (e.g. P.26932) and fragments of *Poraspis* (P.26931) and *Onchus* (P.26934). It was at first thought that these blocks were actually in place (White & Toombs, 1948: 12), but the section contains much down-wash and the probability of their having been carried or fallen from above must be accepted. Fifty feet above these the '*Psammosteus* Limestones' phase is represented by 30 ft. or more of markedly calcareous marls with discontinuous limestones, and above this again sandstones and cornstones have yielded *Pteraspis leathensis* (P.26927–9) and *Poraspis* (P.26930) in place, about 140 ft. above the *T. symondsi* bed. So far no other fossils have been detected in any of these beds, except *Tesseraspis* (e.g. P.26918–19) and a single head-shield of a small *Cephalaspis* [B.U.506], not identifiable as to species, which come from or near the *T. symondsi* bed.

(*c*) Block in road 450 yds. SW. of Lye Mill (and about 1,200 yds. SSE. of Morville Church). *Pteraspis leathensis* (e.g. RP320, 322). No associated fossils.

(*d*) Meadowley Hill, 450 yds. W. of Lye Mill (and about 800 yds. SSW. of Morville Church). In the block with *P. leathensis* were found *Onychodus* teeth (RP315) and fragments of an undescribed Ostracoderm or Arthrodire (RP313).

(*e*) Section at head of Yewtree Dingle 1,180 yds. WSW. of Morville Church. Associated fossils are *Poraspis* sp. (De3907), *Thelodus* scales (De3905*a*, 3906), a ribbed spine (De3906), and *Pachytheca*. Wickham King places this exposure just below the '*Psammosteus* Limestone'; Pocock, 50 ft. above it.

(*f*) Aston Hill, 800 yds. WSW. of Morville Church. *P. leathensis* (e.g. RP303). There are no associated fossils. Wickham King maps this exposure as just above the '*Psammosteus* Limestone', but Pocock places the limestone some 50 ft. lower.

(*g*) Aston Hill Wood, loose blocks in bank side, 500 yds. SSW. of Morville Church. With *P. leathensis* (e.g. De3892) were also found a Cephalaspid (De3897, 3898*a*) and indeterminable ichthyodorulites (e.g. De3899). L. J. Wills has also collected from near here ('¼ mi. SSW. of church') good fragments of *P. leathensis* and one of *Poraspis* sp., and 'in loose blocks on escarpment 500 yds. from church' some nearly complete dorsal and ventral disks of the *Pteraspis*.

8. *Near Brecon*

One, possibly two, specimens found south of Brecon recently by W. N. Croft, are interesting in that their horizons can be clearly related to the *Traquairaspis symondsi* horizon of Crwcas Wood (see White, 1946: 213, loc. 14, 'Crwcws Wood').

In Crwcas Lane, about 300 yds. east of Pen-y-lan farmhouse, 1 mile south of Brecon Castle, a small exposure has yielded a fair example of the ventral disk in counterpart of *P. leathensis* (P.26542–3). The level is about 710 ft. O.D., nearly 50 ft. above a 3-ft. limestone band and perhaps 100 ft. above the *Traquairaspis symondsi* horizon in Crwcas Wood, about ¼ mile to the north-west.

In the old quarry by Pen-y-lan farmhouse, some 300 yds. to the west of the above exposure, a single small fragment, possibly of this species (P.26541), has also been found. The top of the quarry is on the 770-ft. contour, so that the level is some 60 ft. above that of Crwcas Lane.

The record by Wickham King (1934: 541) of *P. leathensis* with '*Psammosteus anglicus*' from the flats on the south side of Caldy Island, Pembrokeshire (see White, 1946: 213), has not been confirmed.

III. PALAEONTOLOGY

As noted above, *Pteraspis leathensis* was recorded long before the species was described, at first as '*Cyathaspis leathensis*' and then under its present designation, and a fair number of specimens, collected by Wickham King from several localities and considered by him to be conspecific, were attributed to this undescribed form and were so labelled. The two most important localities from which such specimens came were 'Leath I' (or 'Leath Stream'; see p. 70 *supra*) and 'stream near Oldfield' which are about 7 miles apart. The first of these two localities was considered to be in Wickham King's stage I. 8, the second in I. 9, but the two series of fossils were generally similar in appearance comprising mostly fragments or isolated plates of a very small *Pteraspis*, black in colour in a grey matrix; and in the original description (White, 1935: 445, text-figs. 30, 31, 38, 77, 94) the two suites of fossils were accepted as being conspecific and the description and restoration based on them jointly. However, subsequent collecting from these, but more especially from other areas, has clearly shown that the fossils from the Oldfield section, which include the elongated rostrum, belong to an unusually small form of another species, *P. crouchi*, and the restoration is therefore a chimaera, *P. leathensis* being in fact a round-snouted form similar to certain Continental and polar species, which are conveniently grouped together as a new sub-genus.

Genus *PTERASPIS* Kner 1847

(*a*) Sub-genus **Simopteraspis** nov.

(Gr. σιμός = snub-nosed)

Diagnosis. Species of *Pteraspis*, generally of small size, with blunt rounded snout. Pineal plate small, more or less triangular and widely separated from orbital plates which are without medial extensions. Cornual plates small and triangular. Interorbital sensory canal forming long V-shaped loop on dorsal disk.

Species. *P. leathensis* White, the sub-genotype; *P. gosseleti* Leriche; *P. primaeva* Kiaer; *P. vogti* Kiaer.

Pteraspis (Simopteraspis) leathensis White

(Text-figs. 2–14, 20; Pl. 5)

1921*b*. *Cyathaspis leathensis* W. W. King, p. 7 (*nomen nudum*).
1925. *Cyathaspis leathensis* W. W. King, p. 387 (*nomen nudum*).
1934. *Pteraspis leathensis* W. W. King, pp. 530, 534 (*nomen nudum*).
1935. *Pteraspis leathensis* E. I. White, p. 445, text-figs. 30, 38, 77, 94 (*non* 31).
1936. *Pteraspis leathensis* F. H. Edmunds & K. P. Oakley, p. 29 (name only).
1947. *Pteraspis leathensis* T. H. Whitehead & R. W. Pocock, pp. 11, 22, 23 (name only).

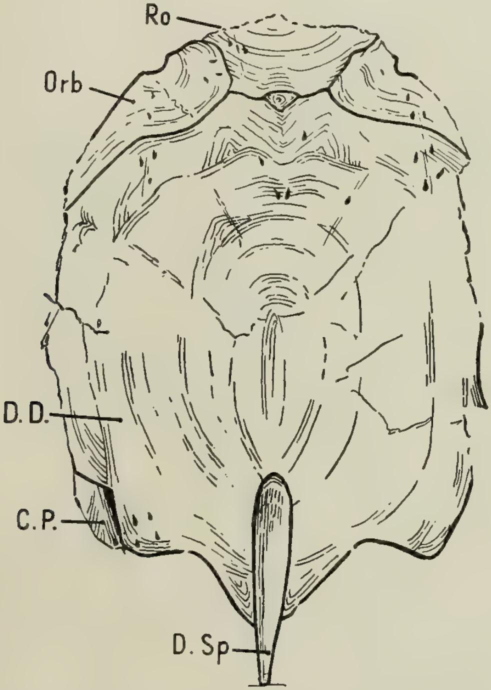
Diagnosis. A *Simopteraspis* with dorsal shield attaining a length of 5 cm. without dorsal spine. Dorsal disk depressed in front but vaulted posteriorly with maximum breadth over curve nearly equal to length from tip of rostrum to end of spine socket; anterior margin of disk very short and usually deeply indented; antero-lateral margins gently concave; posterior margin concave on each side of pronounced median projection pierced by dorsal spine socket, which forms $\frac{2}{7}$ to $\frac{1}{3}$ length of disk and probably exceeds that of exserted portion of depressed, laterally compressed spine. Rostrum short, forming rather more than $\frac{1}{5}$ length of dorsal shield, and about $\frac{1}{8}$ longer than distance between orbital plates. Pineal plate very small, widely separated from orbital plates which have convex antero-medial margins but no medial extension, and slightly exceed in length distance between orbits. Cornual plates triangular, medium-sized, reaching forwards beyond level of spine-socket.

Ventral disk ovoid with short, flattened or emarginated anterior border and convex posterior margin with blunt median angle.

Ridges of external ornamentation numbering 50–80 per cm. and Λ-shaped in section. Variation in form and ornamentation of scales as in *P. rostrata toombsi* but transverse ridges rather more broken up and longitudinal ridges less subdivided posteriorly.

Description. The new material gives an entirely different picture of this important species from that given in the original description, and is almost complete in respect of the carapace. The best specimens are those from Ammons Hill (Text-figs. 3–5, 9), the first of which is the external impression of an almost entire dorsal shield.

This shield, comprising the rostrum, pineal plate, orbitals, dorsal disk, dorsal spine, branchial and cornual plates, is known in detail except for the extremity of the spine. The length of the adult dorsal shield as indicated by the largest specimens from Ammons Hill (Text-figs. 3, 4, &c.) reaches 5 cm. without the spine, and the Leath specimens (Text-fig. 2) are similar in size; but the Porch Brook shields are only three-quarters as large (Text-figs. 6–7) and seem to have relatively larger cornual plates, and more distinct denticulation of the ridges of the ornamentation. These differences may be due to juvenility. The specimens from the Morville area provide intermediate types.



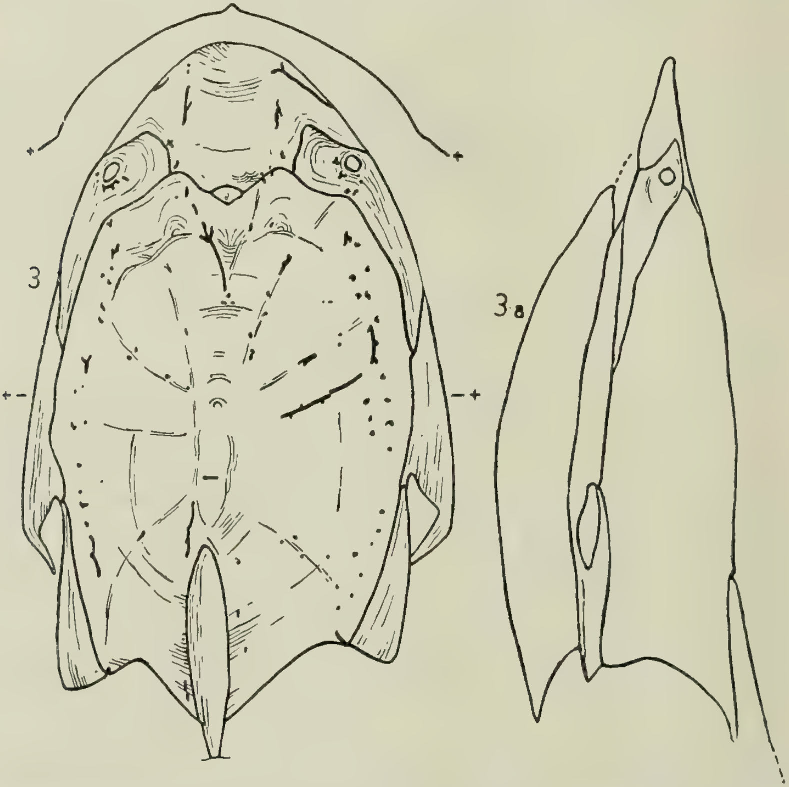
TEXT-FIG. 2. *Pteraspis* (*Simopteraspis*) *leathensis* White. External impression of flattened dorsal shield with imperfect rostral and branchial regions. The holotype, Leath Stream. [P.14521. ×2.]

C.P., cornual plate; *D.D.*, dorsal disk; *D.Sp.*, dorsal spine; *Orb.*, orbital plate; *Ro.*, rostrum.

The rostrum is short and rounded, typical of this group of *Pteraspis*, while its posterior border is undulating to a degree seen in no other British species (Text-figs. 2–6; Pl. 5, Fig. 1). Its breadth between the orbitals is about $\frac{9}{10}$ that of the median length of the plate. The orbital plates, which are widely separated from the small pineal plate, have a sinuous margin with the dorsal disk, of which the antero-lateral corners are cut away, the anterior margin of this plate being very unlike that of other British species, all of which are a simple heart-shape in front. The hinder margin shows a strong median projection pierced by the large socket of the dorsal spine, but the spine itself is laterally compressed and short (Text-figs. 3, 4, 8; P.14522).

The branchial plates are long, and the cornual plates small and narrow in the Ammons Hill specimens (Text-figs. 3, 4), but rather wider and more triangular in those from Porch Brook (Text-fig. 7; Pl. 5, Fig. 2).

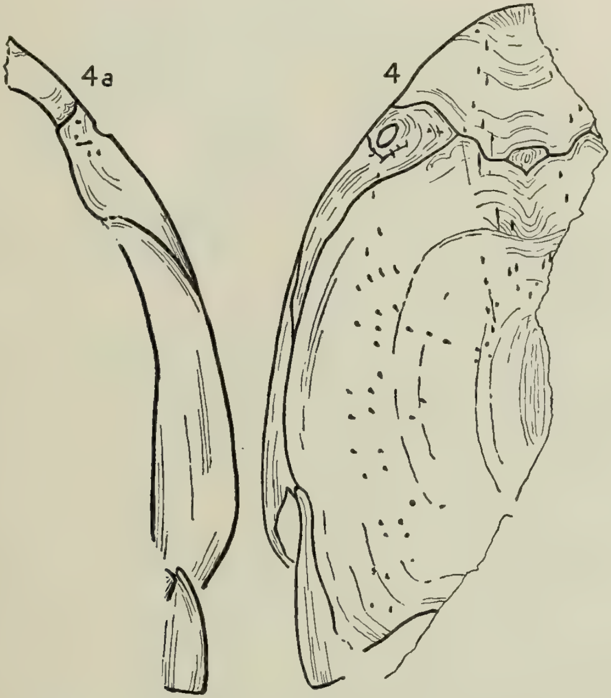
Text-fig. 7 shows a most remarkable specimen, the earliest instance of teratology in a vertebrate animal that I know. It is the left side of a blind monster of the small Porch Brook series in which the branchial and cornual plates seem to be normal, but the hinder part of the orbital is fused with the dorsal disk, although its posterior point is indicated by a notch, and the discrete, anterior portion is triangular and without an orbit. The lower, outer part of the orbital sensory canal also seems to be missing. This abnormality would appear to be due to an injury received at a very early stage, before the plates were formed.



Text-fig. 3. *Pteraspis* (*Simopteraspis*) *leathensis* White. External impression of complete dorsal shield, showing remains of sensory canals and pattern of ornamentation. +––+, cross-profile of internal cast. 3*a*. Side view with ventral disk added. Ammons Hill. [P.23014–5. × 2.]

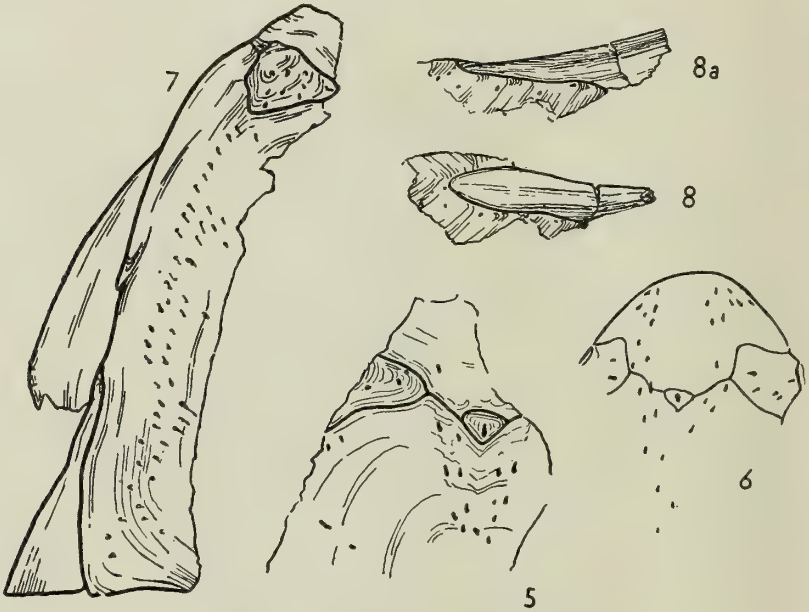
In regard to the ventral disk, little is to be added to the original description (White, 1935: 407, text-figs. 38, 77), but the specimen figured from Ammons Hill (Text-fig. 9) shows a well-developed 'pocket' for the insertion of the anterior ventral ridge-scale. No other plates of the carapace have been found.

Isolated scales (Text-figs. 10–14; Pl. 5, Figs. 3–5) are plentiful at both Porch Brook and Leath Stream, but only the former are well preserved. The same types of scales are found as in *P. rostrata* (White, 1935: 413, text-figs. 56–62, pl. 27) and the anomalous double scales are well represented. The ordinary flank-scales tend to be rather less regularly diamond-shaped and the anterior ridge-scales less pointed than in the bigger species. But the most interesting feature of these scales is their relatively enormous size and the large anterior areas of overlap. In size they are actually about the same size as those of *P. rostrata toombsi* although the shields are only $\frac{2}{5}$ as long, while one of the double flank-scales (RP311) is actually 6 mm. in height and is therefore as large as the giant scales of *P. rostrata* from Trimpley. Whether these scales do belong to the shields with which they are associated may be questioned, for it is possible that they were brought together by water-sorting—but no larger plates of this or any other contemporary species are known from the region.



TEXT-FIG. 4. *Pteraspis* (*Simopteraspis*) *leathensis* White. External impression of right side of dorsal shield. 4*a*. Undersurface of rostrum, orbital, branchial and cornual plates respectively. Ammons Hill. [P.23018. × 2.]

The area of overlap is clearly shown in a number of specimens (Text-figs. 10–14). The surface is often crinkled and the free margin irregular, while the width varies greatly. This area of overlap is also seen in *P.* (*Rhinopteraspis*) *dunensis* (White, 1938, text-figs. 6–9), and it is obvious that such a feature was present in all species, its absence in the numerous specimens of *P. rostrata* (White, 1935) is due to the chances of preservation—which is rather remarkable in view of the superb state of preservation of the specimens from Wayne Herbert and Trimpley. Recently a fresh examination has shown that this feature is partly preserved in one of the Trimpley scales (P.17444).



Pteraspis (*Simopteraspis*) *leathensis* White

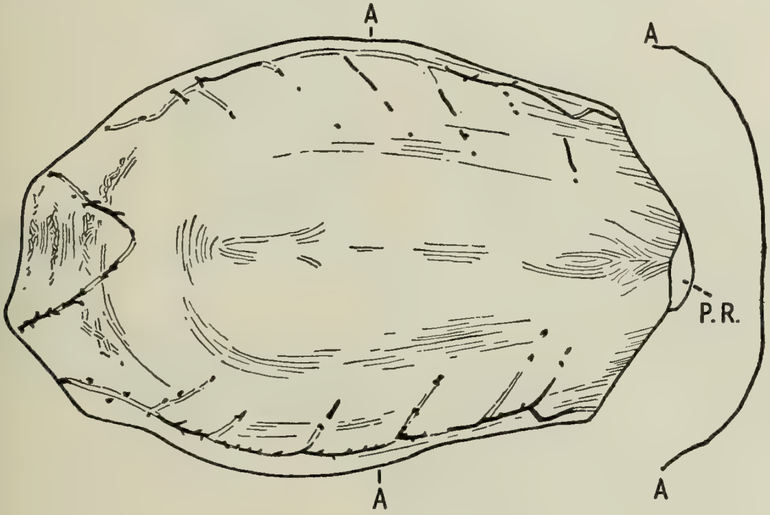
Text-fig. 5. External impression of pineal area of dorsal shield. Ammons Hill. [P.23793. × 2.]

Text-fig. 6. Rostral area of small dorsal shield (see also Pl. 5, Fig. 1). Porch Brook. [B.U.487. × 2.]

Text-fig. 7. Left side of dorsal shield of abnormal, blind specimen without orbit and with hinder part of orbital plate fused with dorsal disk. Porch Brook. [B.U.488. × 3 approx.]

Text-fig. 8. Imperfect dorsal spine and socket, in dorsal and (*a*) lateral views. Porch Brook. [B.U.489. × 2.]

The ornamentation follows the usual pattern of the genus (Pl. 5, Figs. 1, 2) and comes within the usual range of fineness (50–80 ridges per cm.; see White, 1938: 107). The individual ridges are ʌ-shaped in section with fine but conspicuous denticulation when unworn. A feature of this species is the marked irregularity of the ridges at the beginning of the later growth-stages, especially on the dorsal and ventral disks, as indicated by the extreme unconformity between the ridges outside the major-growth lines. In the holotype (Text-fig. 2) two such stages are shown, in the large disks from Ammons Hill only one (Text-figs. 3, 4, 9), but in the little specimen from Porch Brook (Pl. 5, Fig. 1) there is none, which suggests that it is not fully grown. These irregularities seem to indicate the resumption of rapid growth after a resting period. The ornamentation in the antero-lateral marginal area of the ventral disk is often broken up into confused short lengths or tubercles (Text-fig. 9), and in the centre of this plate confused areas are also sometimes to be seen (P.16853*i*).

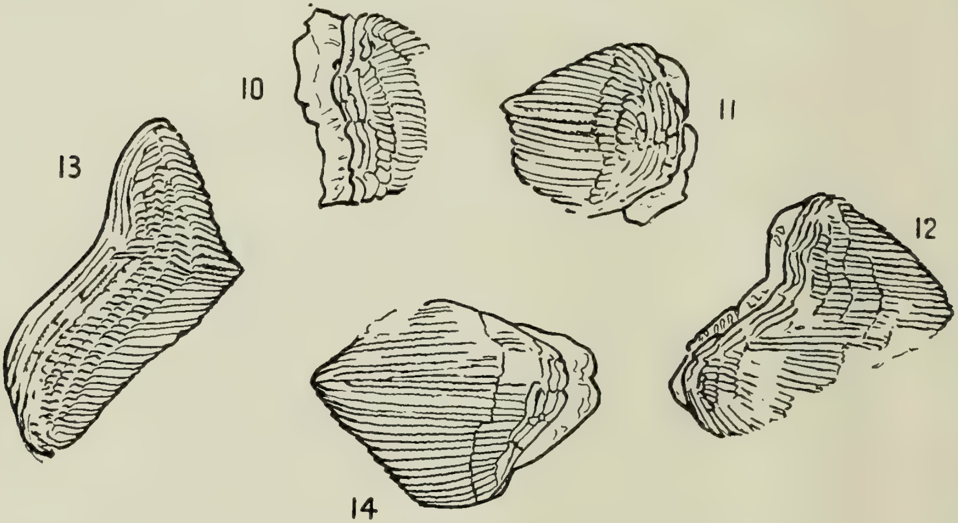


Text-fig. 9. *Pteraspis* (*Simopteraspis*) *leathensis* White. External impression of ventral disk showing sensory canals, with cross-profile of internal cast at A.A. Ammons Hill. [P.23016–17. × 2¼ approx.] *P.R.*, 'pocket' for insertion of anterior ventral ridge-scale.

The ornamentation of the scales resembles that of *P. rostrata toombsi* (White, 1935: 419, pl. 27, figs. 107–9) in that it consists of a series of longitudinal ridges divided in front into short lengths by transverse grooves which are usually preceded by a number of transverse ridges parallel with the anterior margin of the scale (Text-figs. 10–14; Pl. 5, Figs. 3–5)—but both transverse ridges and grooves are fewer than in the *P. rostrata toombsi* (in *P. rostrata trimpleyensis*, on the other hand, the transverse ridges are absent; see White, 1935, text-figs. 56–62).

Of the sensory canal system it may be noted that the 'inter-orbital' canal, instead of running through the pineal plate immediately behind the pineal macula as in other British species in which it is known (see White, 1935, text-figs. 26, 66, 68–9, 81), runs back to form a long V-shaped loop in the dorsal disk, as in the Spitsbergen species *P.* (*S.*) *primaeva* (Kiaer, 1928, text-fig. 1), and in the French *P.* (*S.*) *gosseleti* (Text-fig. 15). It is probably a feature common to all species of the sub-genus. The inner longitudinal canals vary considerably in their position relative to the inter-orbital loop and may be widely separated from it (Text-figs. 2, 3) or run close by it (Text-fig. 4).

Comparison with Other Species. The first of the short-snouted species of *Pteraspis* to be described was *P. gosseleti* Leriche (1906: 26, text-fig. 8, pl. i, figs. 6–9) from the 'Passage Beds' (Psammites de Liévin) of the Pas-de-Calais (see Barrois, Pruvost, & Dubois, 1922: 180–4). Thanks to the kindness of Professor Leriche and Professor Pruvost I have been able to examine these specimens from the collections of the University of Lille. There are four dorsal shields, two of which are nearly complete (Text-figs. 15–17, 19), but the surface of the plates has almost disappeared and very little is left of the ornamentation, so that the outlines of the individual plates are most difficult to determine, especially in the pineal and orbital region. The largest is rather smaller than the Ammons Hill specimens, having a median length of 40 cm., while the smallest is about the size of the Porch Brook series. There seems little or no difference between the French and English specimens in proportions when allowance is made for curvature, but so far as one may judge, the former have a relatively larger pineal plate, a larger base of the dorsal spine, and shorter cornual plates, while the rostrum seems more acute (cf. Text-figs. 19–20). It is, however, not impossible that when well-preserved specimens of *P. gosseleti* are forthcoming the two forms may prove to be conspecific.



Pteraspis (*Simopteraspis*) *leathensis* White

Text-fig. 10. Imperfect left flank-scale with exceptionally large area of overlap. [B.U.492.]

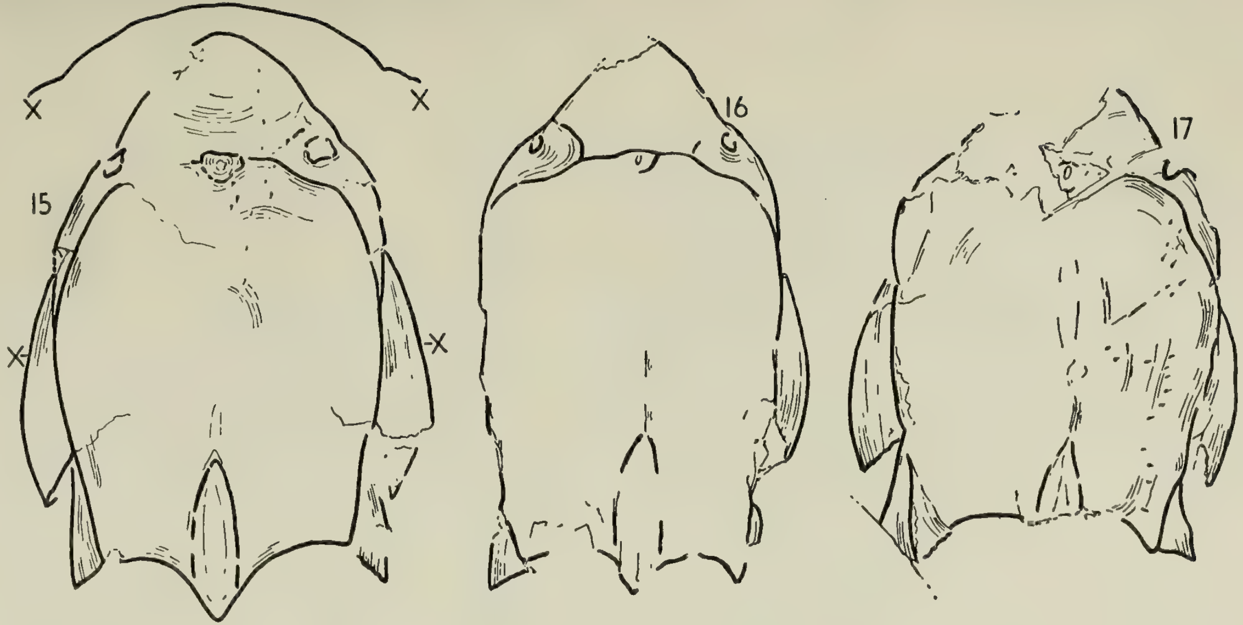
Text-fig. 11. Right flank-scale, probably from near top of series. [B.U.493.]

Text-figs. 12, 13. Double flank-scale, probably from right flank and therefore covering two diagonal rows, but orientation not certain. If inverted each would cover the area of two scales in the same row. In Fig. 13 the area of overlap has been broken away. [B.U.490, RP700.]

Text-fig. 14. Anterior ridge-scale. [RP718.]

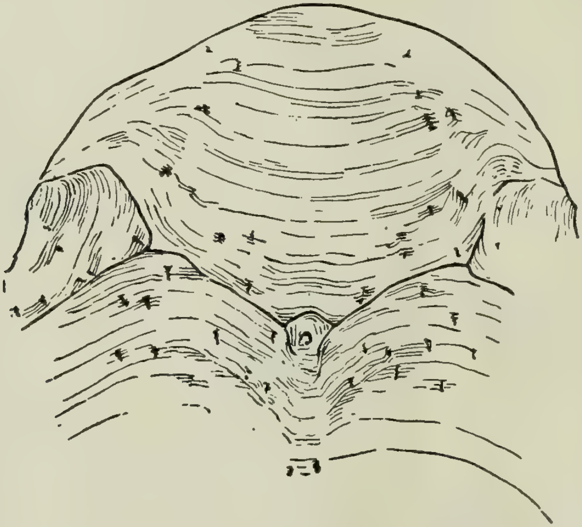
All specimens from Porch Brook. × 8.

Pteraspis vogti has not yet been described and our published knowledge of it is confined to the famous restoration of the undersurface of the carapace showing the mouth-parts and on photographs of this region (Kiaer, 1928: 119, text-fig. 2, pl. xii). Professor Anatol Heintz has, however, kindly compared photographs and drawings



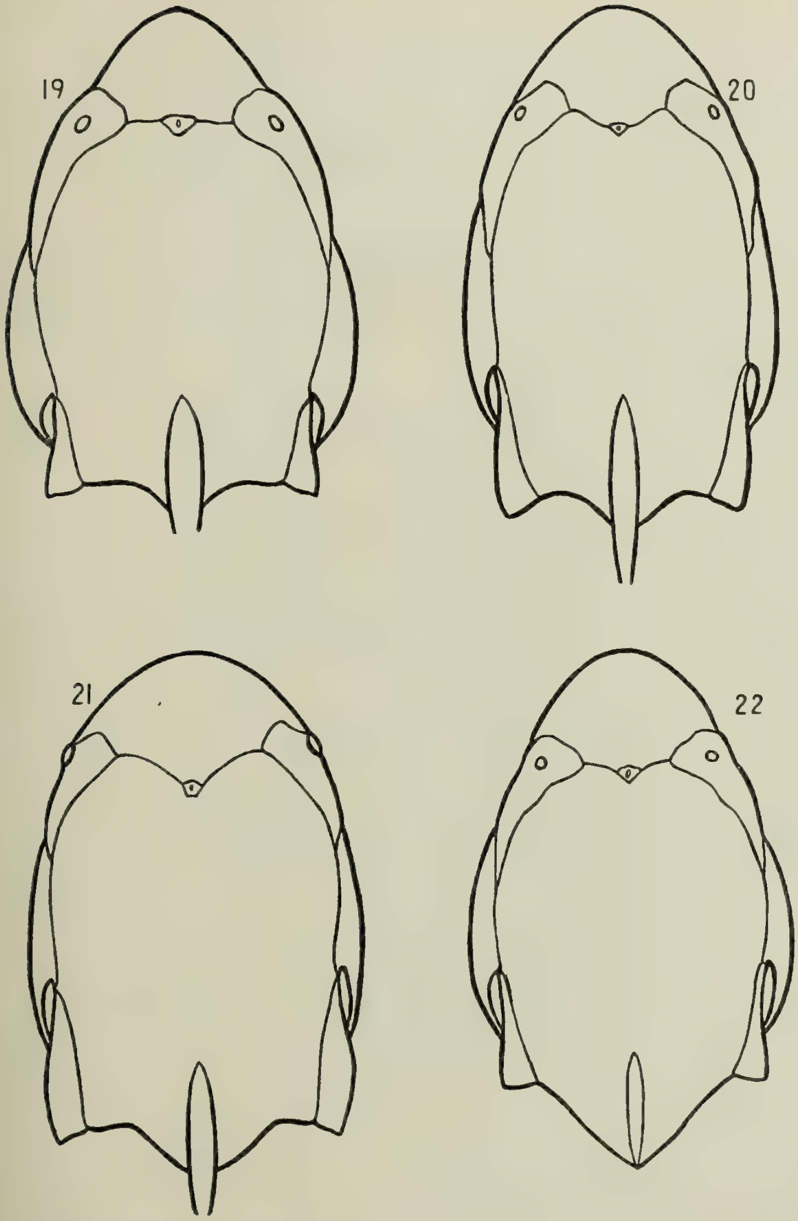
Text-figs. 15–17. *Pteraspis* (*Simopteraspis*) *gosseleti* Leriche. Three of the four syntypes. The original of Fig. 15 is hereby chosen as the lectotype. *x–x*, Cross-profile. Psammites de Liévin, Pas-de-Calais. [Univ. Lille. × 2.]

of *P. leathensis* with specimens of the Spitsbergen species and sent me photographs on which Text-figs. 18 and 21 are based. *P. vogti* attains a substantially greater size than the English species and appears to be somewhat broader and flatter with a shorter and more rounded rostrum, smaller orbital plates, and finer ornamentation. According to Føyn & Heintz (1943: 43) *P. vogti* is known only from the basal layers of the Ben Nevis Division, which they equate with the Dittonian.



TEXT-FIG. 18. *Pteraspis* (*Simopteraspis*) *vogti* Kiaer. Rostral and pineal region, showing external pores of sensory canal system and distribution of ornamentation. Base of Ben Nevis Division, Spitsbergen. [From a photograph by A. Heintz. × 3 approx.]

The second species from Spitsbergen, *P. primaeva*, is also as yet undescribed, but Kiaer (1928, text-fig. 1) has published a restoration of the dorsal shield. Professor Heintz informs me that this species is similar in size to *P. leathensis*, but that the ornamentation is finer. The restoration (Text-fig. 22), which again is based on photographs sent by Professor Heintz and differs in some details from Kiaer's, suggests that the cornual plates are smaller, that the orbitals are smaller and of different shape, and that the posterior angle is much more pronounced and entirely occludes the socket of the dorsal spine, which seems to have been more elevated than in the other species; but what Professor Heintz considers to be most significant is that the inside of the shield clearly shows the impression of the semicircular canals and gill-sacs, as in *Poraspis* and *Anglaspis*, indicating that growth of the plates was much more limited than is normal in *Pteraspis*. *P. primaeva*, Professor Heintz informs me (*in lit.* 11 Sept. 1946), is from the *Poraspis* horizon in the middle of the Fraenkelryggen Division of the Red Bay Series. At the base of the Fraenkelryggen Division both *Corvaspis* and *Traquairaspis* [*Phialaspis*] occur (Føyn & Heintz, 1943: 43), which at once recalls the fauna of Earnstrey Brook in the zone of *T. symondsi* (White, 1946:



Text-figs. 19–22. Restorations of dorsal shields of species of *Pteraspis* (*Simopteraspis*). Fig. 19. *P.* (*S*). *gosseleti* Leriche; × 2. Fig. 20. *P.* (*S*). *leathensis* White; × 1½. Fig. 21. *P.* (*S*). *vogti* Kiaer; × 1⅓. Fig. 22. *P.* (*S*). *primaeva* Kiaer; × 2.

210), so that the middle beds with *Pteraspis primaeva* may be readily correlated with the zone of *P. leathensis* which is here taken as the base of the Dittonian, and thus according to our classification only the lowest part of the Fraenkelryggen Deposits are of Downtonian age.

It is interesting to note that the small ventral disks from the Knoydart Formation of Nova Scotia, to which the name *P. novae-scotiae* has been given (White, 1935: 444), resemble those of *P. leathensis* in size and in the ʌ-shape of the ridges of the ornamentation.

To sum up we may say that the appearance of the blunt-snouted forms (*Simopteraspis*) in the distant Spitsbergen area was at about the same time as in England, while on the other side of the Channel we may with some assurance correlate our '*P. leathensis*' beds (here regarded as the base of the Dittonian) with the beds containing *P. gosseleti* (Psammites de Liévin).

(*b*) **Pteraspis crouchi** Lankester

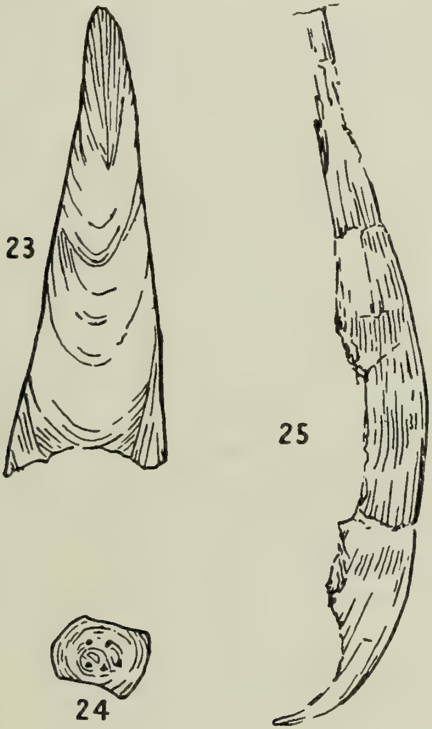
(Text-figs. 23–5)

The original specimens from Oldfield which were ascribed to *P. leathensis* consisted of one rostrum in counterpart, two fragments of rostra, and a lateral plate (P.16851, 2, 4–6). The material which has newly come to hand and which fixes beyond doubt the identity of the species comprises a rostrum (RP461), two imperfect dorsal disks (B.U.333/38, 503), parts of two ventral disks (B.U.500–1), an orbital (B.U.504) and an imperfect branchial plate (B.U.502). Most of the specimens call for little comment except in regard to their uniformly small size, and all are coloured black on a dark grey matrix, very like the specimens of *P. leathensis* from Leath Stream with which they were originally associated. The new rostrum (Text-fig. 23) is defective at the base, but shows the tip which was missing in the original specimen referred to *P. leathensis* and is very slender, measuring over 2 cm. in length and not more than 0·6 cm. across the base as preserved. The other plates are correspondingly small, except the unique polygonal anterior lateral (Text-fig. 24), very like that of *P. rostrata*, which measures 4·5 cm. by 3·5 cm. and seems to belong to an animal three-quarters fully grown, and an anterior piece of the ventral disk representing a fully grown plate some 6 or 7 cm. in length. The branchial plate (Text-fig. 25), like the anterior lateral, is the only known example referable with some certainty to this species. That this plate should be so rare is remarkable, since numerous dorsal shields of this species have been collected within recent years showing the rostrum, pineal plate, orbitals, dorsal disk, and spine all firmly fixed together but never with any evidence of a branchial or cornual plate, whereas in the contemporary *P. rostrata* these are commonly found attached (see White, 1935). The specimen does not differ markedly from the corresponding plate in *P. rostrata*, unless the anterior end, which is imperfect, tapers more. As preserved it is 3·2 cm. long.

No cornual plate has been found in this or among the other plentiful British material, while the single specimen recorded from the Continent (Leriche, 1924, pl. iii, figs. 8, 9) seems too conspicuous a plate not to have been found elsewhere and may not belong to this species. Indeed, one may reasonably expect the cornual plates of

P. crouchi to be even more diminutive than those of *P. rostrata* and the slenderness and length of the branchial plate seems to support this suggestion.

Locality. The specimens came from sections in a stream near 'the Lobby', Oldfield, near Chetton, 4 miles south-west of Bridgnorth. The beds are in a small area determined as stage I. 9 by Wickham King, who separates it by faults from the surrounding rocks, similar in level but referred to stages II. 2–3. However, it seems likely that the stage was determined on the basis of the specimens being misidentified as *P. leathensis*, and there is no reason to suppose that the zone is in fact different from that of the surrounding strata, so that the need for the faults disappears. The section is described by Whitehead & Pocock (1947: 23).



Pteraspis crouchi Lankester
Text-fig. 23. Rostrum lacking proximal end. [RP461.]
Text-fig. 24. Anterior lateral plate. [P.16856.]
Text-fig. 25. Imperfect branchial plate. [B.U.502.]
All specimens from Oldfield. × 3.

Remarks. From no other recorded locality in this country are the specimens of *P. crouchi* so uniformly small; indeed specimens so small as this are altogether extremely rare, and in the British Museum Collection there is only a single dorsal disk from Pool Quarry (P.24468–9) apart from a remarkable series from Cwm Mill, near Abergavenny, discovered by W. N. Croft, in which dorsal disks ranging from less than 2 cm. long (P.25071) to those of fully grown adults three times the size (P.25115) are present. It is interesting to note that in the only two satisfactorily illustrated records of this species outside England and Wales, from the Upper Gedinnian of the Pas-de-Calais (Leriche, 1903, pls. v–vi; 1906: 27, pl. ii) and Belgium (Assise-de-Fooz, Leriche, 1924, pl. iii), most of the specimens are of the same diminutive size as those from Oldfield. The evidence of the Cwm Mill series suggests that these stunted forms are not due to the segregation of half-grown animals, in spite of the absence of growth stages, but to partly uncongenial conditions.

We may appropriately comment here on the range of *Pteraspis crouchi* in general and of its congener, *P. rostrata*.

These two species, as noted above, have never been found in association with *P. leathensis* and the vast majority of their occurrences are in beds clearly above the known range of that species. The range of *P. leathensis*, as previously shown, may possibly include at times elements of the '*Psammosteus* Limestones' phase at its base, but is usually a little higher and continues upwards to constitute a relatively thin zone, possibly up to 70 ft. in thickness; that is to say, in Wickham King's classification, the upper part of stage I. 8 and most of stage I. 9 (see Text-fig. 1). *P. crouchi* and *P. rostrata* are said to be exclusively Dittonian in the original sense (King, 1925: 386), and therefore some 190–300 ft. above the '*Psammosteus* Limestones' (King, 1934: 527). However, at Targrove 2¼ miles north-north-east of Ludlow, *P. rostrata trimpleyensis* (B.M.(N.H.) 35998, 45963–4) has been found in strata about 100 ft. above the '*Psammosteus* Limestones' and 20 ft. below the '*Cephalaspis* Sandstone' shown on King's MS. 6 in. map; while at the Old Furnace Quarry, Bouldon, 6¾ miles north of Ludlow, specimens of *P. rostrata* (Geol. Surv. No. 53303) and Cephalaspids have been found in strata which Wickham King (1925: 385) considered to be in stage I. 9, 100 ft. above the nearest representative of the '*Psammosteus* Limestones'. Moreover, a specimen of *P. crouchi* (P.23772) was obtained between 50 and 100 ft. above the limestones at Pen-y-bwr Quarry, Dorstone, Herefordshire, by H. A. Toombs.

In none of these localities has *P. leathensis* been found, so that the relationships between its zone and that of *P. crouchi* cannot be directly determined, but their relative positions are clear and there is no evidence that they overlap.

The upper limit of the zone of *P. crouchi* is not clear, for the Dittonian becomes marly and more rarely fossiliferous the higher one goes, although some well-known '*crouchi*' localities, like Acton Beauchamp, are fairly high up in the sequence.

Finally, as on many previous occasions, I have to acknowledge the generous assistance given to me by Mr. Wickham King, Professor L. J. Wills (who provided the photographs for the plate), Dr. R. W. Pocock, and Mr. H. A. Toombs; in addition my thanks are especially due to Professor Anatol Heintz, of Oslo, who not only gave me much valuable information concerning the Spitsbergen species, but also sent a fine series of photographs for purposes of comparison; to Professor Maurice Leriche and Professor Pierre Pruvost, through whose kindness I was able to examine the original specimens of *Pteraspis gosseleti* from the collections of Lille University; and to Dr. C. J. Stubblefield, F.R.S., through whose ready co-operation the collections of H.M. Geological Survey have always been accessible to me.

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EXPLANATION OF PLATE 5

Pteraspis (*Simopteraspis*) *leathensis* White

FIG. 1. Flattened fragmentary dorsal shield showing complete rostral and pineal plates and part of both orbitals and median disk. [B.U.487. × 4.]

FIG. 2. Flattened left posterior region of dorsal shield showing cornual plate and part of branchial plate and dorsal disk. [B.U.485. × 4.]

FIG. 3. Posterior ridge-scale lacking posterior (top) end and area of overlap. [B.U.494*b*. × 16 approx.]

FIG. 4. Left double flank-scale. Area of overlap missing. [B.U.494*a*. × 16 approx.]

FIG. 5. Anterior ridge-scale. Area of overlap missing. [B.U.491. × 16 approx.]

[All specimens from Porch Brook; photographs taken by L. J. Wills.]

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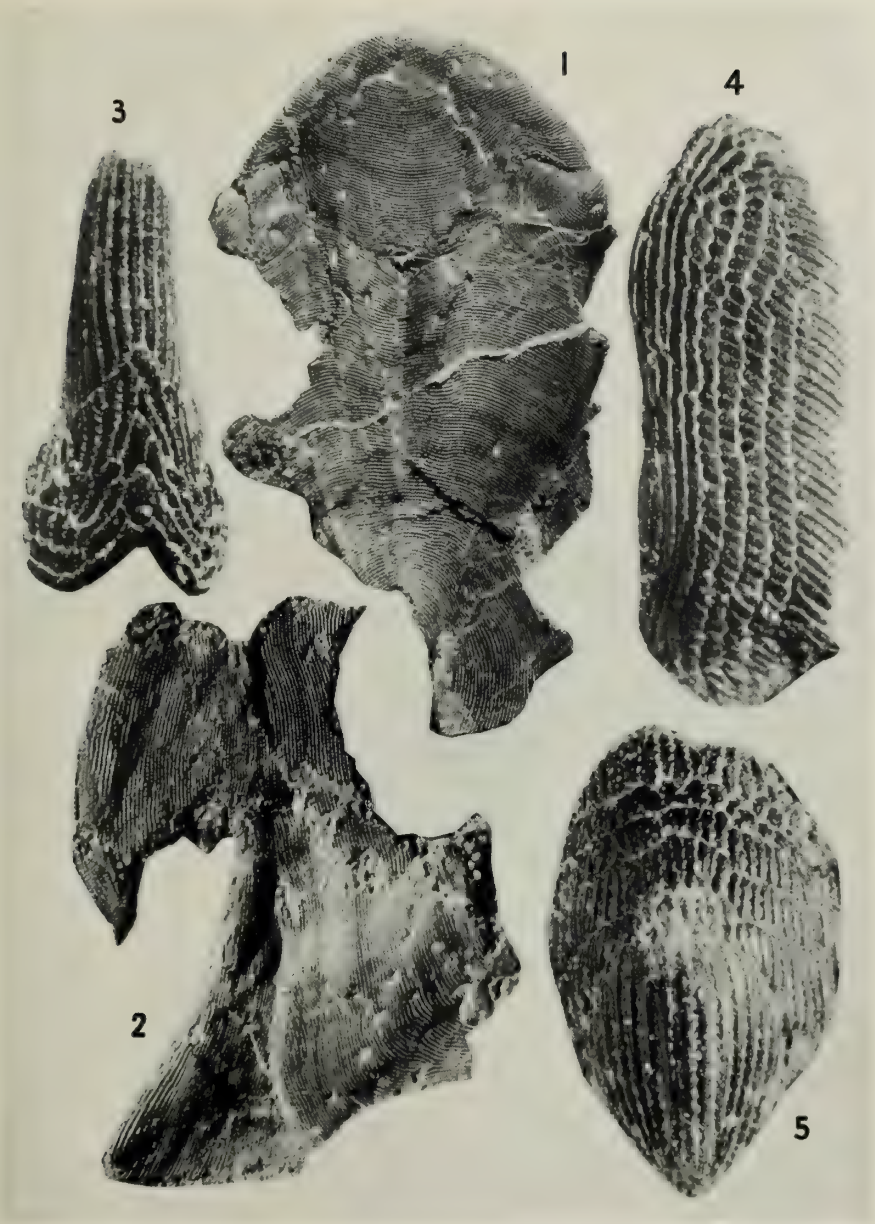

PTERASPIS (*SIMOPTERASPIS*) *LEATHENSIS* White

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GREAT BRITAIN
AT THE
UNIVERSITY PRESS
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BY
CHARLES BATEY
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UNIVERSITY

5 SEP 1950

A NEW TITHONIAN AMMONOID FAUNA FROM KURDISTAN NORTHERN IRAQ

L. F. SPATH

BULLETIN OF
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GEOLOGY Vol. 1 No. 4
LONDON : 1950

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BRITISH MUSEUM NATURAL HISTORY

Pp. 93–146; *Pls.* 6–10

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is to be issued in five series, corresponding to the Departments of the Museum.*

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PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued August 1950 *Price Ten Shillings*

A NEW TITHONIAN AMMONOID FAUNA FROM KURDISTAN, NORTHERN IRAQ

By L. F. SPATH, F.R.S.

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I. INTRODUCTION

The Museum has recently received a fine collection of several hundred specimens of ammonoids from Kurdistan which were presented by the management of the Iraq Petroleum Company Limited. The collection included a particularly interesting Tithonian fauna from one bed in the Upper Jurassic succession on Jebel Gara, near Amadia. A few specimens of this fauna were submitted to me many years ago, including some magnificent examples of entirely new ammonoids. While it was considered most desirable to make this new fauna known to the scientific world, the complete absence of any geological information prevented publication at that time. Now, however, by the kind permission of the Director-General of Economics, Iraq, and the management of the Iraq Petroleum Company Limited, I am in a position to publish the necessary stratigraphical details. An excellent section of the complete Upper Jurassic and Lower Cretaceous succession on Jebel Gara, drawn up by R. Wetzel (who collected the fossils), is available and I can give at least summaries of the various ammonoid faunas of the underlying and overlying beds at that locality, ranging up into the Valanginian. It will be readily admitted that the new Tithonian material is of the highest scientific interest and it is hoped that the present account will form a useful contribution to our knowledge of the fauna of the still somewhat controversial Tithonian stage.

I wish to express my indebtedness to Dr. R. G. S. Hudson for his continued help with information and his interest in the progress of the investigation.

II. STRATIGRAPHICAL SUMMARY

The ammonoids here described come from a bed (*i*) of black bituminous limestone and shale, 33 ft. thick, which is underlain by a considerable thickness (130 ft.) of beds (*d–h*) from which, I am informed, no fossils have so far been collected. Below that (beds *a–c*) the ammonites (including *Ataxioceras inconditum*, *Aulacostephanus* aff. *phorcus*, *Fontannes* sp.) indicate a Lower Kimmeridgian age, so that there must be a large gap in the succession, involving the equivalent of some 850 ft. of Kimmeridge Clay, not to mention the Portlandian and Lower Tithonian stages, if the writer's interpretation of the Upper Jurassic record be accepted (see p. 131).

I am stressing this because the collection contains one fossil, a well-preserved *Hybonoticeras* (better known as '*Waagenia*') of the common *hybonotum* type, that does not fit into the assemblage. It was said to come from the same bed as the other specimens and it has the same black, bituminous limestone matrix; it is also clearly not a derived fossil. But it formed part of an early collection of ammonites which I am informed were 'not collected with the same precision' as the Jebel Gara fossils of more recent collections. *Hybonoticeras*, being one of the most highly specialized ammonites, is unlikely to have had a long range, so that the obvious explanation is that this single Middle Kimmeridgian specimen must have come from some underlying bed, presumed to be unfossiliferous. This would reduce the gap to some extent, but it might be held to support the view of those who place the Middle Kimmeridgian *lithographica* (or *steraspis*) zone, i.e. the horizon of *Hybonoticeras*, immediately below, or even in, the Tithonian.

When discussing the age of the fauna described in these pages in a final chapter, I shall attempt to show that the gap between the horizon of *Hybonoticeras* and the Tithonian is very real. Here it may suffice to repeat that between the *Gravesia* Beds, the home of *Hybonoticeras* (in more southern latitudes), and the base of the Tithonian as here understood, there are 910 ft. of Upper Kimmeridgian and Portlandian strata in England, many of them teeming with ammonites. The Pavlovids of the higher of these beds link up with the *pseudocolubrinus* and *colubrinoides* type of ammonites of the Lower and Middle Tithonian, but have not the remotest affinity with the Berriasellids and other ammonites of the Upper Tithonian.

Above the bed (*i*) that yielded the present fauna follows another bed (*j*), 45 ft. thick, which contains abundant ammonites. Those collected from the scree of this bed, unfortunately all crushed impressions, include *Haploceras*, *Substeueroceras*, and especially *Grayiceras* (= '*Simbirskites*'), similar to forms of the Spiti Shales; but there are as yet no examples of *Berriasella* or late *Parodontoceras* of what we used to call the *privasensis* zone of the uppermost Tithonian. In fact, after an interval of unfossiliferous beds (*k–r*) of no less than 145 ft. in thickness, there follow three more beds (*s–u*) that have yielded Tithonian ammonites. First, the basal bed (*s*), 193 ft. above the main Tithonian assemblage here described, contains a few forms of *Parodontoceras* and at least two genera and a number of new species of uncoiled ammonoids, comparable to some '*Leptoceras*' and '*Ancyloceras*' figured by Mazenot (1939) from the south of France. But as these forms range through the Tithonian and Berriasian up into the Valanginian, they are not of particular value for dating, at least in the present state of our knowledge. On the other hand, the succeeding beds (*t*, *u*), 60 ft. higher, have yielded specimens of *Parodontoceras*, *Berriasella*, and *Protacanthodiscus*. As these are still Tithonian in my opinion and even include a *Berriasella* of the *privasensis* group, they are considered to represent the top of the Jurassic, especially since the next higher bed (*x*), 16 ft. thick and 16 ft. higher in the sequence, included a *Berriasella calisto* (d'Orbigny), complete with aperture and lappet. This last assemblage marks the base of the Cretaceous. It is hoped to describe the ammonites of these higher beds in the Tithonian, and the many new forms of the Berriasian or Infra-Valanginian ('*calistoides*' and *boissieri* zones) in a separate paper.

III. SYSTEMATIC DESCRIPTIONS

Family OPPELIDAE Haug, emend. Spath, 1928

Sub-family STREBLITINAE Spath, 1925

Genus ***OXYLENTICERAS*** gen. nov.

GENOTYPE: *O. lepidum* sp. nov., Plate 6, figs. 1–5.

DIAGNOSIS: Compressed oxycones, with closed umbilicus. Greatest whorl-thickness at umbilical callosity. Almost flat sides, with (typically) only faint striae of growth.

Whorl-section wedge-shaped, with very sharp venter. Suture-line not clearly visible. Body-chamber about half a whorl. Aperture apparently without rostrum.

REMARKS: This Oppelid is obviously different from any Tithonian genus so far described, and although it is as yet incompletely known, it would be misleading to refer it provisionally to *Neochetoceras* or *Streblites*, as I thought of doing at one time. The generic features are those of the genotype described below and it may suffice to state briefly that *Oxylenticeras* has the flat, smooth, and involute shell of *Paralenticeras*, the oxynote venter of *Oxynoticeras*, but the rather finely divided suture-line of the Oppelidae, so far as can be seen, and not of the simplified *Garniericeras* (see Spath, 1947: 14, text-fig. 2).

In its comparatively large siphuncle and half-whorl of body-chamber the genotype species shows some resemblance to *Neochetoceras steraspis* Oppel sp. (1863: pl. lxix, fig. 12), but this has an open umbilicus, crescentic, not straight, outer ribs, and it is not truly oxynote. *'Oppelia' paternoi* Di-Stefano sp. (1884: 31, pl. ii, fig. 12), with a small umbilicus and a sharpened periphery, is another form of *Neochetoceras*. I previously (1925: 117) referred it to *Streblites*, but it also is not closely comparable to the group here described. The other small and oxynote forms of *Neochetoceras* described in geological literature are associated with earlier faunas.

Reference of the present group to *Streblites* would have been still more open to criticism. In the narrower sense, that is as applied to the *tenuilobatus* group, this genus is characterized by the more or less nodate primary ribs; the periodic tubercles of the secondary ribs are less constant. This type of ornamentation is well shown in the original figure (Quenstedt, 1846: pl. ix, fig. 16) and in *S. frotho* Oppel sp. (1862: pl. 1, figs. 1*a*, *b*). It is true that *S. weinlandi* Oppel sp. (1863: pl. liii, figs. 1*a*, *b*) somewhat resembles the form here described, at least in the curvature of the striae of growth; but it still has the *Streblites* keel instead of an oxynote venter.

Substreblites zonarius Oppel sp. which persists, apparently unchanged, from the Tithonian into the Valanginian and perhaps even into the Hauterivian (Spath, 1939*a*: 139) still has the typical *Streblites* aspect, as have the examples before me (of *S. folgariacus* Oppel sp. ?) from the Lower Tithonian *Virgatosphinctes* Marls of Antsalova, Madagascar, as much as the Valanginian *S. ambikyensis*. Besairie sp. (1936: 143, pl. xiii, figs. 16, 17). These forms have the high external lobe of *Uhligites*, but not its distinctive ornamentation and punctate keel; and instead of developing a rounded venter, *Substreblites* retains the characteristic smooth siphonal band which supported the very prominent keel of the test. *Substreblites* is now included in Streblitinae, as well as *Cyrtosiceras* Hyatt, contrary to the opinion expressed in 1925 (p. 115) and 1928 (p. 148) when I doubted the longevity of the Streblitid stock and also wrongly placed *S. motutaranus* G. Boehm (1911: 17, pl. ii, figs. 5*a*, *b*) in *Uhligites*, instead of *Substreblites*.

Another Tithonian Streblitid, namely, *Gymnodiscoceras* Spath, 1925 (= group of *Oppelia acucincta* Blanford sp.), not becoming oxynote and having strongly sigmoidal ribbing, is less closely comparable to the form here described than is *Substreblites*. Whereas the exact range of *Gymnodiscoceras* is still uncertain, a Streblitid that has actually been found in the Middle Tithonian together with *Pseudolissoceras zitteli* is *Oppelia waageni* Zittel (see Burckhardt, 1930: table 11 to p. 112). In 1925 I compared that species to the Somaliland *Neochetoceras simile* Spath, but both lack the sharp venter of the present form, as does *'Oppelia' strambergensis* Blaschke (1911: 154, pl. i, figs. 6, 7) of the Upper Tithonian.

Oxylenticeras lepidum sp. nov.

PLATE 6, FIGS. 1–5

This species is based on the completely septate example figured in Plate 6, fig. 1, which has the following dimensions:

Diameter . .	58 mm.
Height of last whorl	67% of the diameter
Thickness of last whorl	28% ,, ,,
Umbilicus . .	0% ,, ,,

The extremely sharp keel is broken off all round; but it is visible at the beginning of the outer whorl. The periphery shown in the illustration thus is formed alternatively by the solid siphuncle or, where this has fallen out, by the groove in which it lay. The whorl-side is perfectly smooth, partly because in an endeavour to expose the suture-lines the delicate striae of growth were obliterated. There is no suspicion of a spiral groove at the middle of the side, but the interlocking of the elements of the closely packed suture-lines simulates the presence of spiral lines. No individual septal edge, unfortunately, was sufficiently clearly exposed for reconstruction or comparison with the suture-line of other Streblitids or similarly oxynote *Garniericeras*.

A second specimen of 60 mm. diameter (Plate 6, fig. 2*a*) has just over half a whorl of body-chamber, but this is crushed and as in all the other specimens only the septate whorls are solid. These are figured separately in fig. 2*b*, and they well show the delicate ornamentation, consisting of sigmoidal striae on the inner whorl-side which become perfectly straight on the outer half. In another example (Plate 6, fig. 3) from a different locality this ornamentation is slightly more pronounced, and shows a curious resemblance to that of *Oxynoticeras wingravei* Spath (see Wright, 1881: pl. xlviii, fig. 1), except that the umbilical portion of the ribs is more sigmoidal in the present form.

There seems to be some variation also in thickness, and this is not due to the mode of preservation. The greatest whorl-thickness is at the umbilical callosity; it is well seen only in the holotype, which must have been originally of at least 90 mm. diameter. One of the compressed examples figured in Plate 6, fig. 4, has a whorl-thickness of only 23 per cent. at 30 mm. diameter, while what seems to be a more inflated variety (Plate 6, fig. 5) has a whorl-thickness of 26 per cent. at 23 mm. diameter. This last, however, like the more strongly ornamented form (Plate 6, fig. 3) comes from a different locality, so that it is possible that the many smaller oxynote forms here united with the large holotype in one species include distinct variations.

Family HAPLOCERATIDAE Zittel, emend. Spath, 1928[1]

Genus *GLOCHICERAS* Hyatt, 1900

Glochiceras (?) sp. juv. ind.

PLATE 6, FIG. 6

The immature example here figured and several other young specimens are too small for definite identification, but they are obviously different from externally similar inner whorls of *Hildoglochiceras*, e.g. the East African *H. spira* Zwierzycki sp. (1914: 49, pl. v, figs. 11–13). A series of the Madagascan form of *H. kobelli* (Oppel) figured by Besairie (1936: pl. x, fig. 12), which the Museum owes to the kindness of that author, shows how at a diameter of only 20 mm. or less the inner half of the whorl-side changes into a high umbilical slope, bordered by the raised inner edge of the spiral groove. In the present form, on the other hand, the spiral groove is well away from the perpendicular and low umbilical wall and the flattened inner half of the whorl-side is even wider than the outer. This is certainly more reminiscent of the Kimmeridgian *Glochiceras* than the Lower Tithonian *Hildoglochiceras*.

The specimen here figured has a whorl-thickness of 24 per cent. of the diameter (25 mm.), but many species of the two genera mentioned have a similarly flattened whorl-section. The present form, however, has a distinctly tabulate venter which could not have changed to the acute periphery of *Hildoglochiceras*. The ventro-lateral edges are not sharply defined, yet unmistakable, and the narrow venter is absolutely flat, and like the sides perfectly smooth. This ventral flattening is thus quite different from the wide venter developed in some forms of *Haploceras* like *H. carachtheis* Oppel sp., or in the Valanginian *Neolissoceras grasianum* (d'Orbigny). Unfortunately the suture-line is not visible.

This form is more evolute than Oppel's original Kimmeridgian *Amm. nimbatus* (1863: 191, pl. lii, figs. 5*a*, *b*), the genotype of *Glochiceras*, but similar species seem to occur right through the Upper Jurassic, as Steuer's record of Oppel's species from the Argentine Tithonian shows. The latter form may be as distinct from the original *G. nimbatum* as it is from the smooth species here described; but it is interesting to note that there are two impressions in the collection from Shiranish Islam that may be compared to the Argentine form. One (C.41108) has the anguliradiate and comparatively strong striae of growth unprojected on the venter, that is to say, the outer half of the ribs runs up to the periphery in a straight line. In the other example (C.41189) only the lateral bend in the striae of growth was conspicuous enough to leave its mark on the impression of the smooth side. This type of ornamentation is found in some forms of *Brightia* (see *Amm. hecticus* in Quenstedt, 1849: pl. viii, figs. 1*a*, 4*a*); only the knee-bend there is almost tuberculate, distantly spaced and combined with outer ribs, i.e. altogether more extreme than the feeble ornamentation of these forms of *Glochiceras*. These two examples, however, may well belong to two other forms of the genus.

---

[1] The genotype of *Haploceras* is *Amm. elimatus* Oppel, and a recent attempt by Breistroffer (1947) to apply that name to the Cretaceous *grasianus* group and to substitute a new generic name for the typical Tithonian species must be rejected. Favre in 1873 did not emend the genus *Haploceras* Zittel. He merely cited three French species, with the name of one misspelt, as 'examples'. This citation has no legal standing; apart from that it did not even include one of the typical Tithonian species which had been especially characterized by Zittel as representing the acme of development in *Haploceras*. According to Article 30, II. *g* of the Rules, the meaning of the expression 'select the type' is to be rigidly construed. 'Mention of a species as an illustration or example of a genus does not constitute a selection of a type.' The family-name Haploceratidae therefore remains unchanged.

The present species, on the contrary, is much like the small *Amm. erato*, figured by d'Orbigny (1850: pl. 201, figs. 5–6 only), though this is more compressed laterally, has the spiral groove nearer the umbilicus, and lacks the ventral flattening.

Glochiceras (?) sp. nov.

PLATE 6, FIG. 7

The body-chamber fragment here figured is interesting on account of its resemblance to a similar terminal portion figured by R. W. Imlay (1939: pl. iv, fig. 10) and referred to his *G. diaboli*. The latter fragment is even larger and it has a much more pronounced lateral bend in the lines of growth and the ribs, almost as in *Hildoglochiceras*, but it comes from the Kimmeridgian (*Idoceras* beds). Its venter also is broadly rounded so that the resemblance is probably accidental. The forms of *Hildoglochiceras* figured by the same author, e.g. *H. grossicostatum* Imlay (1939: pl. iii, figs. 1–7, 9–11) may thus be more closely related to the present species than the example of *G. diaboli* above cited; yet they also have a more angular radial line. In the form here discussed there is no trace of a spiral depression at the lateral angularity of the striae of growth and ribs which are parallel to the mouth-border. The flattened inner half of the whorl-side is thus entirely different from the wide and steep umbilical slope of the typical *Hildoglochiceras latistrigatum* (Uhlig) and *H. kobelli* (Oppel) from the Spiti Shales.

Since the periphery is damaged, generic identification must remain uncertain. It is perhaps improbable that the present fragment represents a large *Semiformiceras* of the type of *Oppelia microps* (Oppel), figured by Zittel (1870: pl. xxviii, fig. 15), large examples of which might be expected to develop a ventral groove, instead of the row of beads, and to become smooth.

The East African *Haploceras priscum* Zwierzycki (1914: 50, pl. v, figs. 5, 6) might have developed a body-chamber with the coarse ornamentation of the present form, if it grew to that size. The resemblance to the Kachh *Glochiceras ? propinquum* (Waagen) with which Zwierzycki compared his species, is only superficial (see Spath, 1928: 158).

Genus *PSEUDOLISSOCERAS* Spath, 1925

Pseudolissoceras zitteli (Burckhardt)

PLATE 6, FIGS. 8*a–c*

1903 *Neumayria zitteli* Burckhardt, p. 55, pl. x, figs. 1–8.
1907 *Neumayria zitteli* Burckhardt: Haupt, p. 200, pl. vii, figs. 3*a*, *b*.
1925 *Pseudolissoceras zitteli* (Burckhardt) Spath, p. 113.
1926 *Haploceras* (*Pseudolissoceras*) *zitteli* (Burckhardt) Krantz, p. 436, pl. xvii, figs. 4–5.
1928 *Pseudolissoceras zitteli* (Burckhardt): Krantz, p. 18, pl. i, fig. 6.
1931 *Pseudolissoceras zitteli* (Burckhardt): Weaver, p. 401, pl. xliii, fig. 291.
1942 *Pseudolissoceras zitteli* (Burckhardt): Imlay, p. 1443, pl. iv, figs. 1–4, 7, 8, 11, 12.

The Kurdistan examples show such good agreement with the Argentine types that specific identity is suggested. The specimen figured in Plate 6, fig. 8*a*, and a slightly larger example (figs. 8*b*, *c*) have the following dimensions:

Diameter . . .	27 mm.	32 mm.
Height of the last whorl .	51%	51% of the diameter
Thickness of the last whorl	32%	31% ,, ,,
Umbilicus . . .	20%	21% ,, ,,

Both are casts and entirely smooth, but the first example retains a part of the crushed outer whorl, showing faint and almost straight ribs, like the large specimen figured by Krantz. The suture-line is visible on both examples, but only in parts. It differs from that figured by Burckhardt in having a larger second lateral lobe, like that of the more evolute *P. planiusculum* Zittel sp. (1870: pl. xxviii, fig. 3). The external lobe, seen in only one place, is shallow and the proportions of the elements are remarkably similar in the three forms, even if the external saddle seems to be slightly lower and broader in the examples here figured.

There are over twenty specimens, but most of them are smaller than the two here figured and some are only impressions. At 10 mm. diameter the whorl-section is only slightly higher than wide and at 5 mm. it is circular while the umbilicus is comparatively open. In a few of the small individuals there is the merest suspicion of a spiral groove, as in so many other Haploceratids. There is no sign, however, in any of the specimens, of a depression, just outside the prominent umbilical edge, as shown in Haupt's fig. 4. The present examples, in fact, all belong to what has been called the variety with the more inflated whorl-section, figured in Haupt's fig. 3.

The impression of an unusually large example (No. C.41188), comparable to that figured by Krantz in 1928, seems to agree with it in most respects, so far as can be seen. Only the lateral bend in the radial line is slightly more marked and the striae are more pronounced near what appears to have been the mouth-border at about 115–120 mm. diameter. The lateral angularity of the radial line, it may be added, is not nearly so distinct as in *Haploceras elimatum* Oppel sp. (in Zittel, 1868: pl. xiii, fig. 7) and the presence of an umbilical rim is in favour of comparison with *Pseudolissoceras*. But in view of the discovery of a *Hybonoticeras* in the same collection (p. 96) it is not impossible that the impression belongs to a form of *Glochiceras* of the *fialar* group of the Kimmeridgian. It therefore has to be left indeterminate.

Pseudolissoceras advena sp. nov.

PLATE 6, FIGS. 9, 10; PLATE 8, FIG. 10

This form is almost a homoeomorph of the Argentine Middle Tithonian '*Oppelia*' *perlaevis* Steuer (1897: 73, pl. xx, figs. 7–9), but it has a larger umbilicus and a distinct umbilical edge, also a suture-line that suggests reference to *Pseudolissoceras*. Steuer gave the whorl-height of his species as 44 per cent. of the diameter, but this is less than the (possibly inaccurate) drawing shows. According to Krantz (1928: 14) the height may be as much as 58 per cent., at least in a comparable Andine form, whereas in the holotype of *P. advena* here figured (fig. 9*a*) the whorl-height is 50 per cent. The width of the umbilicus is correspondingly greater (19 per cent. instead of 10 or 12 per cent.), while the whorl-thickness is only slightly less (25 per cent. instead of 27–28 per cent.). The sides are flat and almost smooth, the striae of growth being extremely fine, and there are occasional irregular folds, as in Steuer's species. The holotype has two *Beudanticeras*-like constrictions, faint but distinct enough for one to be marked even on the periphery.

At 16 mm. diameter the whorl-thickness is 37 per cent. and the evenly arched venter is comparable to that of '*Oppelia*' *perglabra* Steuer (1897: 74, pl. xxi, figs. 13–15) which, however, has no umbilical edge and more sigmoidal striation. The holotype is entirely septate and therefore could well have been as large as Steuer's largest example of his '*Oppelia*' *perlaevis*.

A specimen from Shiranish Islam (fig. 10) of possibly a slightly different age (see p. 132) has a diameter of 49 mm. and an umbilicus that seems larger because the slope is steep and the edge is very distinct. The whorl-section is also thinner (although the specimen is partly crushed), at least at the periphery, all characters in which the variety of *P. zitteli* with high and compressed section figured by Haupt (1907: 200, pl. vii, fig. 4) differs from the holotype of *P. advena*. It will be noticed that the suture-line of Haupt's Andine form is more complex than that of the typical *P. zitteli*. In the holotype of *P. advena* the suture-line is slightly corroded (see Plate 6, fig. 9*a*) but also less simplified than in *P. zitteli*, although of the same pattern. There is a similar shallow external lobe, a broad, bifid saddle, and two wide lateral lobes. The small size of the first lateral saddle alone is against reference of this form to *Haploceras*. Since the suture-line of the Shiranish Islam example above mentioned is slightly more complex than that of the holotype of *P. advena*, it may perhaps be looked upon as a transition from the Haploceratid main-stock to *Pseudolissoceras*.

A smaller example of 26 mm. diameter (figs. 9*c*, *d*) differs from the holotype chiefly in having no constrictions, but it is slightly malformed, the umbilical rim with its spiral depression being less conspicuous on the side not figured. A second Shiranish Islam specimen of 34 mm. diameter well shows the very fine Phylloceratid striation, but it has no umbilical edge, which makes it look different from the other specimens; its simple suture-line (Plate 8, fig. 10), with asymmetrical ventral lobe, is that of *P. advena*. It may be a variety corresponding to the typical forms of *P. zitteli*, without umbilical rim.

Uhlig (1903: 38) considered it uncertain whether Steuer's '*Oppelia*' *perlaevis* was related to *Streblites* (*tenuilobatus* group) because the suture-line 'permitted of various interpretations'. Steuer's drawing of the suture-line is obviously not very accurate, but it is a *Haploceras* suture-line, though it may be noted that Uhlig did not refer the species to that genus. Apart from the suture-line, the *Beudanticeras*-like whorl-shape of the present form, with a tendency of the whorl-sides to converge, not diverge, as in many species of *Haploceras*, suggests a different stock. Since the suture-line of the form here described is that of *Pseudolissoceras*, if more complex, the similarity in whorl-shape to '*Oppelia*' *perlaevis* is not considered of any significance.

Genus *LAMELLAPTYCHUS* Trauth, 1927

Lamellaptychus sp. ind.

PLATE 10, FIG. 12

The single pair of *aptychi* in the collection, about 30 mm. long and embedded in a piece of shale so as to show the striations of the concave sides, can be compared to the two *aptychi* in the body-chamber of a *Neochetoceras steraspis* figured by Oppel (1863: pl. lxix, fig. 2). The broader end, however, differs in having the striae much less curved, where they meet the internal edge, whereas in Oppel's figure and in numerous specimens in the Haeberlein collection in the Museum these striae are very strongly curved.

This comparative straightness of the lineation suggests comparison with *L. crassissimus* Haupt, as figured in Weaver (1931: pl. 58, fig. 371, enlarged) and Trauth (1936: pl. iii, fig. 13, natural size); but the massive *aptychus* of Haupt's original figure (1907: pl. viii, figs. 3*a*, *b*) described as *Punctaptychus* is not at all like the present example. Another comparable form is *Aptychus* sp. figured by Steuer (1897: pl. xxiv, fig. 3) from Cineguita I, i.e. from below the *zitteli* zone in Burckhardt (1930); and the association of this with Haploceratids as well as with *lamellaptychi* of the *beyrichi* type suggests that the *aptychi* belonged to some form of *Haploceras*. An indeterminable, flattened impression of a Haploceratid, in fact, occurs on the same slab of shale as the pair of *aptychi* here described.

Whereas the example just referred to comes from Shiranish Islam, an impression of a pair of minute *lamellaptychi* is said to be from the Ammonite Bed on Jebel Gara; only it has a Perisphinctid in the same piece of matrix that may be Kimmeridgian. The *aptychi*, in any case, are too small to be identified, even if they were of Tithonian age.

Family PERISPHINCTIDAE Hyatt, 1900

Sub-family VIRGATOSPHINCTINAE Spath, 1931

Genus ***PHANEROSTEPHANUS*** gen. nov.

GENOTYPE: *P. subsenex* sp. nov. (Plate 7, figs. 5*a*, *b*).

DIAGNOSIS: More or less evolute shells with arched venters and inner whorls like *Virgatosphinctes*. On the outer whorls, however, the costation tends to disappear, both on the periphery and on the sides, until only umbilical bullae remain. Greatest whorl-thickness therefore gradually moves from the middle of the whorl-side to umbilical border. Slope steep, but rounded. Varying number of shallow and almost straight constrictions. Body-chamber about two-thirds of the last whorl. Mouth-border with a broad, shallow contraction, apparently confined to the sides, but with ventral lappet. Suture-line complex at first, tending to simplify at the end; broad, unsymmetrically bifid external saddle and irregularly trifid first lateral lobe, as deep as the external lobe or deeper. Second lateral lobe and two auxiliary lobes short and oblique, as in *Sublithacoceras*, but simpler (Plate 7, fig. 6*b*).

REMARKS: I was at first inclined to compare one of the forms now included in this new genus (*P. hudsoni* sp. nov.) with a group of Somaliland ammonites (genus

Pseudoclambites Spath, 1925) provisionally attached to the family Aspidoceratidae. Apart, however, from the fact that both genera tend to lose their ornamentation and develop smooth outer whorls, the resemblance is not very close. The inner whorls are different so far as can be seen and there is no suggestion of a ventral sulcus in *Phanerostephanus*, such as is shown in *Pseudoclambites costatus* Spath (1935: pl. xxv, fig. 6) as well as in the two species described in 1925.

The holotype of *Phanerostephanus*, however, has decidedly more affinity with the genus *Sublithacoceras* Spath, 1925, which also has Virgatosphinctid inner whorls, but tends to lose the ribbing altogether, instead of developing umbilical tubercles. A form like *S. dacquei* Schneid sp. (1915*a*: 359, pl. xxvi, fig. 3) might be considered intermediate in this respect, but the genotype, *S. penicillatus* Schneid sp. (1915*a*: 329, pl. xviii, fig. 3) shows that the ribbing is completely lost, even if the primaries do not disappear until after the secondary ribs. There is, of course, the difference in size, and the suture-line of *Sublithacoceras* is very complex, has numerous pendent auxiliaries, and a very deep and symmetrical principal lobe.

The true *Virgatosphinctes* Uhlig, i.e. the *broilii*-group, as restricted in 1931 (Spath: 463) also loses its ribbing, but only at very large diameters, and before that the ribs tend to unite in bundles. In *P. subsenex*, on the other hand, the 'Pseudovirgatitid' ribbing with its characteristic constrictions is much more like that of the Neuburg species of *Sublithacoceras*; and in appraising the systematic position of *Phanerostephanus* the almost total absence of a ventral groove or smooth zone seen in *Virgatosphinctes transitorius* or *Sublithacoceras senex* (Oppel) is considered as significant as the presence of umbilical nodes on the body-chamber of *P. subsenex* as well as in the extreme *P. hudsoni*. Moreover, *Phanerostephanus* is connected by transitions with the new genus *Nothostephanus*, as mentioned below (p. 114), and their affinities, whether Virgatosphinctid or Virgatitid, are, in my opinion, certainly not with the Berriasellids *Dalmasiceras* or '*Neocomites*' of the *occitanicus* group, though these have comparable umbilical tubercles. *Phanerostephanus*, in short, is a Perisphinctid, and not a Berriasellid. It may be a modified offshoot of the same stock that produced *Virgatosphinctes transitorius* and its allies, the last representatives of the group in the Tithonian, but it has no 'Hoplitid' features.

Phanerostephanus subsenex sp. nov.

PLATE 6, FIG. 15; PLATE 7, FIGS. 5–7

This species is based on the example figured in Plate 7, fig. 5, the (restored) dimensions of which are as follows:

Diameter . . .	97 mm.
Height of the last whorl	?42% of the diameter
Thickness of the last whorl	?36% ,, ,,
Width of the umbilicus .	38% ,, ,,

The whorl-section is ovate, with slightly flattened sides and an evenly arched venter. The inner whorls are more depressed and bear bifurcating ribs with the secondary branches slightly projected on the venter. After about 25 mm. diameter triplicate ribs appear, with the anterior branch coming off at a lower level than the remaining two secondaries and followed by a constriction, inclined forwards and succeeded by a single rib. There may also be pairs of bifurcating ribs, joining at the umbilical edge, or even bi- and trifurcating ribs, uniting just before a constriction. At 50 mm. diameter the branching becomes somewhat less clearly defined, owing to the flattening of the sides; and at the end of the septate stage (64 mm.) the secondaries tend to disappear while the primary ribs develop blunt bullae and become more distantly spaced. The body-chamber occupies about two-thirds of the outer whorl and its sides and venter are perfectly smooth. The mouth-border is almost intact on the side not figured and is preceded by a faint ridge, followed by a constriction, but the ventral lappet is broken off. The suture-line is visible near the end of the septate portion and is more complex than that of *P. hudsoni*, without apparent simplification.

The smaller example figured in Plate 7, fig. 6, has its last half-whorl crushed accidentally and the early constrictions seem rather oblique, but like a third and similar specimen (fig. 7) it probably belongs to the same form. They might easily be taken for the inner whorls of a Perisphinctid like *P.* aff. *transitorius* (Oppel) figured by Burckhardt (1903: 40, pl. v, figs. 7–9) for, according to that author, even typical Stramberg examples of Oppel's species may lack the characteristic ventral sulcus on the earlier whorls. The obvious distinction then is the projection of the peripheral ribbing in *Phanerostephanus*. It may be added, however, that a young and therefore doubtful, although solid and well-preserved specimen (pl. 9, fig. 7; no. C.41185) has a ventral sulcus that disappears at a diameter of about 20 mm. This small example and an impression (No. C.41190) may represent a compressed variety of *P. subsenex* or even a new species, transitional to *P. intermedius*, only less closely ribbed.

Steuer's badly drawn Argentine example of *Amm. transitorius* (1897: 32, pl. xxix, fig. 6), significantly referred to *Reineckeia*, is not closely comparable to the form here described; but Toucas's larger Chomérac specimen of his *Perisphinctes transitorius* (1890: 599, pl. xvi, figs. 5*a*, *b*) differs chiefly in retaining regular bifurcation to a later stage. *Perisphinctes chalmasi* Kilian (1889: 652, pl. xxviii, fig. 1) from the Lower Tithonian of Andalusia may possibly represent a development comparable to the form under discussion, tending to umbilical tuberculation and smooth outer whorl; but it lacks the typical constrictions and its comparison by Kilian with much earlier (Kimmeridgian) species may not be so inept as the occurrence 'with *P. transitorius*' suggests.

One crushed example (No. C.41200) which to a diameter of about 25 mm. appears to be much like the young *P. subsenex* figured on Plate 7, fig. 6, has the peripheral ribs extremely projected on the outer whorl (diameter = just over 40 mm.); but this sudden change in the costation is so unnatural that it can only be due to oblique crushing. It certainly gives the ammonite the appearance of a *Kossmatia*, but in reality the form is believed to be a transition between *Phanerostephanus* and *Nothostephanus*. Its affinities with the latter are indicated by the fact that the triplicate ribs have the longest branch behind the bifid pair instead of in front, as in *Phanerostephanus* and most of the other Upper Jurassic Perisphinctids.

After the present account was already completed and too late for incorporation in the text or the plates, an example of a new *Phanerostephanus* reached me which is almost exactly half-way between *P. subsenex* and *P. hudsoni*, but is also distinctly transitional to the more involute *Nothostephanus*. It has about three-quarters of the outer whorl belonging to the body-chamber, at just over 100 mm. diameter, and its proportions (100–41–31–33) are intermediate between those of the two species mentioned. But the specimen was one of an assemblage found loose (with other species and at least one Lower Kimmeridgian *Ataxioceras*) at Rowanduz and Zakho, Iraq.

Phanerostephanus hudsoni sp. nov.

PLATE 8, FIGS. 1, 2

The complete holotype of this species (No. C.40746) has the following dimensions:

Diameter . . .	66 mm.
Height of the last whorl	38% of the diameter
Thickness of the last whorl	30% ,, ,,
Width of umbilicus .	42% ,, ,,

To the diagnostic features already mentioned in the generic description it may be added that although the whorl-section is widest at the umbilical tubercle, the ventral portion is broadly arched, not compressed, and the sides are only slightly convergent. The test is extraordinarily thick near the aperture, but not where it is flaking off on the venter (fig. 1*b*). The suture-line is not seen in the holotype, but the siphuncle is exposed on the first third of the outer whorl, to the second constriction. This is not so deep as the first, though more distinct than the third. These constrictions are only slightly inclined forwards and the anterior rim is more pronounced than the posterior. There is only a very slight ventral sinus, so that the constrictions are convex forwards on the periphery.

The suture-line is well exposed on the fragment (No. C.40749) illustrated in Plate 8, figs. 2*a*, *b*, which is entirely septate and thus belonged to an example considerably larger than the holotype. In the still larger species described above as *P. subsenex*, with a somewhat less simple suture-line, the costation remains to a diameter of 60 mm., but the inner whorls are believed to be more or less identical. In the present form the change begins already at about 25 mm. diameter, though the ventral costation is visible to 35 mm. After that, especially between the first and second constrictions of the outer whorl, only a few indistinct and irregular striae seem to meet at the umbilical bullae and probably represent lines of growth since the cast is entirely smooth.

Phanerostephanus intermedius sp. nov.

PLATE 8, FIGS. 3, 6; PLATE 10, FIG. 11

Only the inner whorls of the holotype are here figured since the outer whorl is badly crushed. The figure thus represents the septate stage and only the beginning of the body-chamber. At that stage the dimensions are:

Diameter . . .	49 mm.
Height of the last whorl	37% of the diameter
Thickness of the last whorl	28% ,, ,,
Width of the umbilicus .	36% ,, ,,

The remainder of the crushed body-chamber is preserved as an impression, representing over half a whorl, so that the size of the complete specimen was approximately 75 mm. The whorl-section is compressed laterally, with almost parallel sides and an evenly arched venter. The ribs are strongly inclined forwards in the umbilicus, rather irregular, and there are occasional oblique constrictions. On the last whorl of the septate stage the ribs are rather closely spaced, especially the secondaries which result from the bifurcation and trifurcation of the primaries. In the trifurcating ribs the anterior branch is the lowest, but even the remaining two branches bifurcate lower down on the whorl-side than the intervening biplicate ribs. All the ribs are fairly sharp and well defined, with the anterior slope less steep than the posterior. There are about four constrictions to the whorl, apparently getting shallower towards the beginning of the body-chamber. The latter has the secondary ribs somewhat less closely spaced than before and they are only slightly projected forwards on the periphery. The points of furcation become indistinct, but it is only near the aperture that the ribs of the lateral area degenerate and lose their regularity. No umbilical nodes are visible as the inner part of the body-chamber has been crushed on to the unfigured side of the septate whorls represented in Plate 8, fig. 3*a*.

The suture-line has a large, unsymmetrically bifid external saddle and a deep external lobe, with a high median saddle. The first lateral lobe is trifid but less deep than the external lobe. Its deepest part is already beyond the middle of the whorl-side. The lateral saddles and the auxiliaries are apparently like the corresponding elements in *P. hudsoni* (fig. 2), but not clearly exposed. The suture-line on the whole is comparable to that of *Virgatosphinctes transitorius* (Oppel) as figured in Zittel (1868: pl. xxii, fig. 4), but the lateral saddles are less elongated.

The only other solid example (No. C.41192), part of an ammonite of about 80 mm. diameter, has the characteristic fine and sharp costation, but this is slightly more inclined forwards. What remains of the outer whorl includes apparently the last septal edge. Although there are primary ribs on the umbilical shoulder of this outer portion, the sides and periphery are smooth, probably owing to corrosion, for the venter retains a few secondary ribs where the beginning of the body-chamber is crushed in and escaped erosion. The slender whorl-section, comparable to that of *Kossmatia desmidoptycha* Uhlig (1910: pl. xlvii, fig. 2), is typical, but what resemblance there may be to the genus *Kossmatia* (genotype: *K. tenuistriata* Gray sp.) is due chiefly to the sharpness of the fine ribbing.

This species is less completely known than the typical *P. subsenex*, but this is partly due to accidents of preservation. It appears to be the commonest species of the genus. There are many impressions similar to that figured in Plate 10, fig. 11, which do not show the later smooth stage and therefore could be the young of *Virgatosphinctes* of the *transitorius* group. But the impressions having a diameter of more than 40 or 45 mm. (Plate 8, fig. 6) begin to show loss of lateral ribbing, like the form described below as *P. dalmasiformis* sp. nov. It is not certain, in view of slight differences in the closeness of the ribbing, that all the impressions belong to one species and its varieties. Thus the last example here figured (Plate 8, fig. 6) is, perhaps, somewhat transitional to *P. dalmasiformis*. It shows at least ten constrictions on the outer whorl, a feature which is reminiscent of many of Schneid's Neuburg species of

Sublithacoceras, or of a Somaliland specimen of *Pseudovirgatites* I figured on a previous occasion (Spath, 1925: 136, text-fig. 4).

Phanerostephanus dalmasiformis sp. nov.

PLATE 8, FIG. 7

This form, unfortunately, is represented only by crushed examples including the type here figured, but apart from the whorl-thickness and the suture-line they show most of the external characters that make this species an interesting link between the genotype, *P. subsenex*, and *P. intermedius* on the one hand and the more specialized *P. hudsoni* on the other. The inner whorls show the fine ribbing and periodic constrictions of *P. intermedius*, but only to a diameter of about 25 mm. Then the costation becomes irregular and faint, except at the umbilical edge. On the outer whorl the ribbing has almost disappeared, on the side as well as the venter, while even the umbilical nodes become less distinct. There are two faintly prorsiradiate constrictions visible on the outer whorl, bordered by ribs on the periphery; the side is entirely smooth and was probably originally evenly rounded, not so flat as it now appears. The diameter is approximately 60 mm., unless the whorl-section was as inflated as in *P. hudsoni*; but there is the umbilical border of at least another quarter of a whorl.

The resemblance of the present form to certain species of *Dalmasiceras* is superficial, for the inner whorls are Perisphinctid, not Hoplitid, i.e. the ventral ribbing is not interrupted by a median groove or even a smooth zone. There may be more affinity with *Sublithacoceras glabrum* Schneid sp. (1915*a*: 337, pl. xxii, fig. 1), but the two forms are difficult to compare, not only on account of the difference in size, but also because of the defective preservation. *P. intermedius* sp. nov. (Plate 8, fig. 3) retains its costation to a much larger stage and shows fine peripheral ribs on the body-chamber still at 75 mm. diameter. In *P. subsenex*, at that stage, the venter is also already smooth, although the Perisphinctid aspect is retained to a much larger size than in the present form.

Genus ***NANNOSTEPHANUS*** gen. nov.

GENOTYPE: *N. subcornutus* sp. nov. (Plate 10, fig. 7).

DIAGNOSIS: Micromorph Perisphinctid derivatives in which the point of bifurcation of the ribs on the ventro-lateral edge is tuberculate. But degeneration soon sets in, the concave periphery becomes arched, the horns disappear, and the ventral ribs near the aperture are strongly projected, as in *Proniceras*. The suture-line is not clearly seen in any example, but is very simple.

The innermost whorls are finely ribbed, as in the *colubrini* and other Perisphinctids, and rather depressed, with a broad venter which soon becomes flat and then concave. The secondary ribs on the periphery may zigzag from side to side at this stage, but later ventral projection appears. Since all the twenty examples known of the typical species are of about the same size and since some show a complete aperture and modified ornamentation on the body-chamber, it is clear that they are fully grown ammonites.

Remarks: Since the genera *Aulacosphinctes*, *Micracanthoceras*, and *Corongoceras* have been included in Himalayitinae, it might be thought that *Nannostephanus* is an early member of the same sub-family, though in the more typical Himalayitids the tubercles persist to much later stages. But the absence of a ventral furrow seems to show that the new genus is still closer to the Perisphinctid root-stock than to the later derivatives above mentioned.

The true *Aulacosphinctes* (restricted to the *mörickeanus* group), on account of its deep median furrow on the periphery, does not show zigzagging of the ventral ribs which occurs in the present genus. *Micracanthoceras* and *Corongoceras* seem more like *Nannostephanus*, but only superficially, being far more advanced, and the later stages are scarcely more comparable than the young. Certain forms of *Himalayites*, e.g. *H. cortazari* (Kilian), that have no ventral sulcus and thus are probably less advanced than the commoner types of the group of *H. seideli* (Oppel), are also quite different from *Nannostephanus*, in the young as well as the adult.

When I first saw these small ammonites, I was impressed by the fact that together with *Cochlocrioceras turriculatum* sp. nov. they were the commonest fossils in the fauna here described. But I took them to be inner whorls of some larger genus, like *Windhauseniceras* Leanza, 1945. The outer whorls, in that genus, however, return to a Perisphinctid aspect so different from the early tuberculate stage that Leanza even compared his genus to *Subplanites* and other, earlier, Perisphinctids. Unfortunately there is no material for dissection, but in any case the Argentine example of *W.* cf. *internispinosum* (Krantz) figured by Leanza (1945: 23, pl. xxi, fig. 6) is too badly preserved to be compared with the small forms here described. '*Aulacosphinctes*' *windhauseni* Weaver (1931: 412, pl. 44, fig. 300) retains the *Crendonites* aspect to a considerable diameter, but its inner whorls, to judge by the description, are apparently similar to the specimens of *Nannostephanus* in the present fauna.

There is nothing in the collections before me that could represent an outer whorl of *Windhauseniceras*. In fact there is only the *Aulacosphinctes*-like micromorph form described below as *Nannostephanus* sp. ind. (Plate 6, fig. 12) which is probably related to the typical *N. subcornutus*; but it is interesting to note that the only other ammonites here dealt with, having any resemblance to *Nannostephanus*, are *Proniceras* sp. nov. ? ind. (Plate 10, fig. 6) and the immature whorls of a transitional form attached to *Nothostephanus* (Plate 7, fig. 8). It is not believed that there is a close connexion between these genera, except a common Perisphinctid ancestry, but being a micromorph and transitional to *Phanerostephanus* as well as to *Nothostephanus*, the present genus is not easy to place.

According to Weaver (1931: 420) *Windhauseniceras internispinosum* occurs at the base of the Upper Tithonian, though on p. 46 he has a zone of *W. internispinosum* as the equivalent of the whole of that sub-stage. Leanza (1945) also had the same zone at the base of his Upper Tithonian. In view of the occurrence of *Nannostephanus* together with *Pseudolissoceras* (of the top of the Middle Tithonian ?) it seems clear that the present genus is not a micromorph derivative of *Windhauseniceras*.

The genus *Dickersonia* Imlay, 1942, somewhat resembles *Nannostephanus*, but it also returns to a perisphinctoid outer whorl, after an early spinose stage. The latter, however, as in the nearly allied *Corongoceras*, has peripheral as well as lateral tubercles.

Examples of *Dickersonia* of the size of the specimens here described are thus entirely different and the genus is much closer to the Himalayitinae than is *Nannostephanus*.

Nannostephanus subcornutus sp. nov.

PLATE 10, FIGS. 7–10

The best of the twenty specimens available is that figured in Plate 10, fig. 7, and there is only one impression of a somewhat doubtful, larger example of about 25 mm. diameter which is represented in fig. 8 (from a plasticine squeeze). The most conspicuous feature of the new form is the sharp spine at the ventral edge on the ribs of the inner whorls, where they branch into secondaries that run across the flat and wide periphery with a slight median sinus directed forwards. The peripheral spine (or horn, where well preserved) is lost already at about 17 mm. diameter when the venter becomes arched rather than concave. Though the larger cast does not show the whorl-shape, the ribs seem to pass across an arched venter without a conspicuous peripheral shoulder.

At a diameter of 4 mm. the shell, at first smooth, is finely ribbed, there being about twelve primary ribs on the last half-whorl to eighteen secondaries. The venter at this '*celsus*'-stage is broad and widely arched; the very depressed whorl-section (thickness = 56 per cent.) just begins to show a ventral edge. The spines at this edge then gradually increase to a maximum at 12–15 mm. diameter, but often seem more prominent when seen in the umbilicus, because when exposed and viewed ventrally, they may appear to be merely sharp ribs, unless they are very well preserved. They then may be actual horns, projecting sideways as well as upwards. The secondary branches of the ribs on the slightly concave venter pass irregularly from side to side and occasionally join up with a single rib on the opposite side to form a zigzag pattern.

Something like this is shown, in a less extreme form, on the periphery of *Windhauseniceras internispinosum* Krantz sp. (1926: 453, pl. xiv, figs. 1–2; 1928: 39, pl. ii, figs. 3–4), though owing to its larger size and the presence of trifid ribs, with the spines moved down to almost the middle of the whorl-side, the ventral aspect is different. In the present form, when the venter has become arched, there may also appear (at least in the doubtful cast, fig. 8) trifid ribs and even one quadrifid primary, succeeded by a single costa and a trifid rib, but the point of branching is no longer prominent.

Nannostephanus sp. ind.

PLATE 6, FIG. 12; PLATE 8, FIG. 5

The specimen here figured is very poorly preserved, but it is interpreted as a development of the same dwarf-stock that also produced *Nannostephanus subcornutus*, a stock that may be connected with the more orthodox '*Aulacosphinctes*' *colubrinoides* Burckhardt sp. (1903: 57, pl. x, figs. 9–11) from the Middle Tithonian of Argentina. The '*colubrinoides*'-stage, however, in the present form persists to only about 18 mm. diameter, presumably the end of the septate portion of the ammonite. Later the point of bifurcation of the ribs moves lower down the whorl-side, the ribs are more closely spaced, more inclined, and actually crowded near the aperture. At the same time the ventral sinus of the ribs, directed forwards, becomes pronounced on the body-chamber until, near the ventral lappet of the mouth-border, the peripheral projection is as extreme as in *Proniceras*. There is no trace of a siphonal interruption of the ribs, as in somewhat similar young *Micracanthoceras*. The suture-line is not exposed and the body-chamber is assumed to occupy the last half-whorl only because the aperture is intact, at least ventrally.

I was at first inclined to refer the present form to *Aulacosphinctes*, not because it belongs to the *mörickeanus* group to which the genus was previously restricted, but because forms of the *colubrinoides* type have also been included in that genus, or even in *Crendonites* Buckman (see Spath, 1925: 145; 1936: 31). Moreover, there is a certain resemblance to the earlier *A. colubrinus* (*non* Reinecke) figured by Steuer (1897: 62, pl. xxix, fig. 11). This also has the ribbing continuous across the periphery, at least on the outer whorl; as it otherwise agrees with the typical *Aulacosphinctes* much more than does *A. colubrinoides*, it could be considered a forerunner of the Upper Tithonian species of the *mörickeanus* group. *A. colubrinoides*, according to Burckhardt (1930: table xi), comes from above the zone of *Pseudolissoceras zitteli*, so that Steuer's form which comes from below may not have a sulcate periphery, even in the young. *A. pseudocolubrinus* (Kilian), in which species Blanchet (1928) included both Steuer's *A. colubrinus* and Zittel's Rogoznik form (1870: pl. x, fig. 6), also has the merest suspicion of a ventral furrow in the young, but I have not seen the illustration of any example of these forms with the change in ribbing near the mouth-border which is characteristic of the present example. It is thus much more probable that the latter belongs to the micromorph stock here separated as *Nannostephanus* and that the absence of spines at the point of branching of the ribs on the earlier whorls is only due to the bad preservation.

A somewhat doubtful second specimen (No. C.41129), unfortunately only 11 mm. in diameter, is figured in Plate 8, figs. 5*a–c*. The thickness is considerably greater than the whorl-height throughout; but the venter is evenly arched and appears to be flat, as in the young *N. subcornutus*, only at the beginning of the last whorl. At the same time the point of bifurcation of the ribs at the ventral edge is projecting sideways, though not actually cornute, and the resemblance to the young of the form just cited is not very close. In '*Aulacosphinctes*' *kossmati* Uhlig (1910: pl. xxxvii, fig. 3) the projecting point of bifurcation of the ribs is retained on the outer whorls, but the venter is then still more rounded. In young *Aulacosphinctoides* from the Spiti Shales and the *Virgatosphinctes* Marls of Andranosamonta, Antsalova, &c. (Madagascar), the point of bifurcation of the ribs is prominent, but the venter is rounded even on the innermost whorls. These, however, are all sulcate in the siphonal line, unlike the present form. It is possible that this second example is the young of a more Aulacosphinctoid form.

Sub-Family VIRGATITINAE Spath

This sub-family (at first, 1925, proposed as a family) is now used in its original connotation; for the sub-family 'Pseudovirgatitinae', separated from it in 1931, was based on the genus *Pseudovirgatites* Vetters, and there is some doubt about the affinities and the range of that genus. I had previously considered the genotype *P. scruposus* (Oppel) from the Klentnitz Beds of Niederfellabrunn to be related to *Pectinatites* Buckman, from the Upper Kimmeridge Clay, implying that its inclusion in the Stramberg fauna was due to some error, perhaps a deceptive similarity of matrix. I am certainly at a loss to account for the extraordinary resemblance, even in suture-line, of the 'Tithonian' *P. seorsus* (Oppel) and the 'Volgian' *P. quenstedti* (Michalski) to *Pectinatites aulacophorus* Buckman, from the Upper Kimmeridge Clay, unless they are related. In other words, *Pectinatites* may be a synonym of *Pseudovirgatites*.

On the other hand, Burckhardt (1930) recorded *P. scruposus* from the beds with *Substeueroceras multicostatum*, his highest zone in the Tithonian, and since this would make the range of that species abnormally long, even if my interpretation of the Tithonian (p. 131) be rejected, it may be suggested that there is a later Jurassic stock, homoeomorphous with the Kimmeridgian *Pectinatites* (or *Pseudovirgatites*?). Leanza (1945) indeed confirmed this in referring to *Pectinatites* (with a query) the Upper Tithonian *Reineckeia striolata* Steuer; and another form with resemblance to the species of *Pectinatites* above cited is Steuer's *Perisphinctes densistriatus* (1897: 62, pl. xv, figs. 8–10). In any case, the genus *Pseudovirgatites* and therefore the sub-family Pseudovirgatitinae remain of uncertain standing.

Finely ribbed Perisphinctids, of course, were developed repeatedly, from the Middle Kimmeridgian *Lithacoceras* (*ulmensis* group) up to the Tithonian *Sublithacoceras* (*senex* group), and I mentioned before that if *Pseudovirgatites* itself should be less closely allied to *Pectinatites* than I thought, a different grouping might become necessary. But I am not in a position to suggest more than a few minor changes in the classification of the incompletely known Perisphinctids of the late Jurassic. Thus, while adding one more to the genera previously (1931: 468, 1936: 18) recognized in the sub-family 'Pseudovirgatitinae', I may point out that the young of *Pectinatites* are as different from the Tithonian forms here described as they are from the immature true *Virgatites* or the closely allied *Zaraïskites*. The Kimmeridgian *Pectinatites*, in fact, may well be left in the parent-stock, Virgatosphinctinae, for it is probably a development of its immediate forerunner, *Subplanites* which includes some of the prolific '*contiguus*' group.

As regards the other genera of the former sub-family 'Pseudovirgatitinae', the genus *Anavirgatites* Spath is closely related to what I had considered to be typical *Pseudovirgatites*, i.e. the Upper Tithonian elements, and though they are not boreal types, they may well be classed with the Virgatitinae. The genus *Parapallasiceras* Spath, based on *P. praecox* Schneid sp., ranges from 'Pseudovirgatitid' forms like *P. ciliatum* Schneid sp. to other species of '*Berriasella*' described by that author which have decided leanings towards *Pallasiceras* and the Pavlovinae. I do not consider that this group of '*Berriasella*' *praecox* has close connexion with the Berriasellidae, the forerunners of the Neocomitidae, except of course a common derivation from a Perisphinctoid root. The less modified forms of the '*ciliata* group' are indeed close to the '*colubrini*' which persisted more or less unchanged throughout the Upper Jurassic and gave rise to the Pavlovinae as well as to the true *Aulacosphinctes*. Schneid himself stated that he was inclined to look upon his forms of '*Berriasella*' rather as Perisphinctids than as Hoplitids, whereas Mazenot (1939) identified with Schneid's species Upper Tithonian and even Cretaceous (Berriasian) forms that may be true Berriasellids but, to me, bear no close resemblance to the Neuburg types.

Apart from the genera *Pseudovirgatites*, *Anavirgatites*, *Parapallasiceras*, and *Sublithacoceras*, so far mentioned, the Virgatitinae also include *Pseudinvoluticeras* Spath, and in view of what is said below (p. 115) about the close affinity between that genus and *Nothostephanus* gen. nov., the latter similarly is now referred to the same sub-family. *Nothostephanus* is connected by intermediaries with the new genus *Phanerostephanus* discussed above, although an extreme form of that genus (*P. hudsoni*) seems far removed from either Virgatosphinctinae or Virgatitinae. *Phanerostephanus* is now included in the former sub-family, but as the more typical species like *P. subsenex* also resemble *Sublithacoceras* (*senex* group) and retain the Perisphinctid aspect only to a comparatively small diameter, *Phanerostephanus* could perhaps equally well have been included here. The transitions between that genus and *Nothostephanus*, unfortunately, are represented only by crushed impressions but appear to comprise at least two distinct species. One (C.41167, 41182) is a more evolute edition of *N. kurdistanensis* with Perisphinctid, not Virgatitid inner whorls. That is to say, there are more numerous volutions at a given diameter, with the umbilical width increased to about 33 to 35 per cent. (instead of 22 per cent.) and the umbilical wall low and not sharply defined (compare the inner whorls of Plate 7, figs. 1–3, with those of fig. 6). The second transition has already been referred to under *Phanerostephanus subsenex* (p. 105).

Umbilical tubercles, developed in *Pseudinvoluticeras*, *Nothostephanus*, and *Phanerostephanus*, and only just indicated in *Sublithacoceras*, are really more characteristic of Olcostephanidae than of either Virgatitinae or Virgatosphinctinae. The classification of the transitional types here adopted is thus not entirely satisfactory; but to link these typically Jurassic forms with the essentially Cretaceous *Dalmasiceras* or any other Berriasellid would be still less acceptable.

Genus ***NOTHOSTEPHANUS*** gen. nov.

GENOTYPE: *N. kurdistanensis* sp. nov. (Plate 7, figs. 1–4).

DIAGNOSIS: Fairly involute platycones with high whorls, narrowly rounded venter, and flat sides. Greatest thickness at umbilical nodes on edge of high and steep umbilical slope. Innermost whorls to about 7 mm. diameter rather evolute, with whorls as wide as they are high and simple, distant costation, consisting of single and bifurcating ribs, almost as in *Nannostephanus* (p. 109). One specimen (Plate 7, fig. 8) indeed is transitional to that genus, but at 13 mm. diameter it assumes the typical aspect of the other young specimens (figs. 3, 4), so far as can be seen. At this stage the whorls flatten, the umbilicus narrows, and the ribs become more closely spaced and show irregular branches, with the anterior or posterior branch of the trifid ribs coming off rather low on the whorl-side as in true *Virgatites*. At 30 mm. the ribbing begins to weaken laterally and it becomes difficult to distinguish the branches from merely intercalated secondaries. The ventral sinus, directed forwards, is prominent and there is no sign of a siphonal flattening or interruption of the costation. At 50 mm. diameter the crescentic umbilical portion of the primary ribs is distinctly raised, though true inner nodes are not developed until a diameter of 90 mm. is reached. The secondary ribs then seem to disappear and on the body-chamber probably only the blunt and rounded umbilical tubercles remain. There are indistinct constrictions at irregular intervals; there may be three or four on some of the younger examples, but the holotype only shows one at the beginning of the outer whorl and a very faint constriction, preceded by a raised rib, about half a whorl farther on. In one impression the position of the aperture is marked by a strong constriction, but its ventral portion is not preserved.

The suture-line is characterized by a broad, bifid external saddle, a trifid lateral lobe, about as deep as the external lobe, and two more saddles on the whorl-side which are considerably more slender than those of the simplifying last suture-line shown in fig. 1*a*. The auxiliaries beyond the umbilical tubercle are not visible, but the suture-line as a whole is only slightly pendent towards the umbilicus.

REMARKS: When I first saw the ammonite here described as the holotype of *N. kurdistanensis*, I was struck by its resemblance to *Odontoceras anglicum* Steuer (1897: 165, pl. xxx, figs. 15–17), but that species is a Lower Kimmeridgian *Aulacostephanus* and there could be no real affinity, apart from a common ancestry in a Perisphinctid root-stock. When many years later I examined numerous young examples of the same species, it became clear that the development was entirely different in the two stocks and that there was equally little in common with another superficially similar group, namely, that of *Amm. occitanicus* Pictet (1867: 81, pl. xvi, fig. 1; 1868: 248, pl. 39, fig. 1). This form, which I previously (1939*a*: 62) described as an involute development of *Subthurmannia boissieri* (Pictet) but which Mazenot (1939) included in *Neocomites*, differs from the genus here discussed not only in its ventral groove, which persists to a comparatively late stage, but especially in its suture-line. In *Nothostephanus* this is simplified at the end, but before that it is about as complex as the suture-line of *Dalmasiceras dalmasi* Pictet sp. (in Djanélidzé, 1922: 267, text-fig. 3), only this has a much deeper lateral lobe. *Nothostephanus*, moreover, has constrictions; the ribbing is continuous across the venter even in the earliest stages, and if *Amm. progenitor* Oppel (in Zittel, 1868: 99, pl. xviii, figs. 3*a–d*) is a Tithonian forerunner of *D. dalmasi* of the Berriasian (Mazenot, 1939: 144), then the new genus here described is entirely distinct from *Dalmasiceras*.

There is probably greater affinity of the present genus with *Pseudinvoluticeras* than with any other described forms, especially since the suture-line of *P. somalicum* Spath (1925: 142, text-fig. 10) is very similar to that of *N. kurdistanensis*, before simplification sets in. *P. decipiens* Spath (= '*Simbirskites*' *payeri* R. Douvillé, *non* Toula, 1910: 18, pl. xix, fig. 3) is closer to the present form than either *P. somalicum*, the genotype, or *P. douvillei* Spath, and although its whorl-section still shows the inflated shape characteristic of '*Holcodiscus*' *wilfridi* R. Douvillé and the other two species of *Pseudinvoluticeras*, the lateral aspect is similar. A form that may be identical with *Pseudinvoluticeras douvillei* was described by Weaver (1931) as *Virgatosphinctes lotenoensis* Weaver and referred to the Lower Tithonian; but its near ally *V. windhauseni* Weaver (1931: 425, pl. 48, figs. 324–5) may also be related to the genus *Nothostephanus* and being Middle Tithonian (zone of *Pseudolissoceras zitteli*) is probably of about the same age.

It is believed that the compression, resulting in a narrow periphery in the present form as in the true *Virgatites virgatus* (v. Buch), is responsible for the pronounced ventral sinus of the ribbing. The presence of constrictions, as in *Pseudovirgatites*, enhances the similarity between *Pseudinvoluticeras* and the genus here discussed. If the latter, however, be connected by real transitions with *Nannostephanus* (Plate 7, fig. 7), the position of *Nothostephanus* within the Virgatitinae is somewhat doubtful, though this may indicate no more than derivation of both genera from a Pavlovid ('*colubrinus*') stock.

Nothostephanus kurdistanensis sp. nov.

PLATE 7, FIGS. 1–4, 8

The holotype of this form (fig. 1) has the following dimensions:

Diameter . . .	90 mm.
Height of the last whorl	47% of the diameter
Thickness of the last whorl	27% ,, ,,
Width of the umbilicus .	22% ,, ,,

Since the generic diagnosis given above is based on the present species, there is little to add here, except that the small portion of body-chamber shown in fig. 1*a* is crushed. Assuming the complete body-chamber to have occupied at least another half-whorl, the total diameter of the shell must have been about 130 mm. There are at least another thirty examples of this form, but they are mostly crushed impressions except for some inner whorls, forming a solid core to the impressions. There are slight differences in the closeness of the ribbing (compare figs. 2, 3), but these are trivial. The immature original of fig. 4 (enlarged ×2) has the typical costation from the start. Another similar young individual (fig. 8), however, retains the biplicate stage, with ventro-lateral spines, to a larger diameter than the typical specimens and at first sight might be taken to belong even to a different genus. It is probably a transition to the form described above as *Nannostephanus subcornutus*. Nothing like this change in ribbing is seen on the inner whorls of *Virgatites* or *Zaraïskites* before me, although at about 20–30 mm. diameter they may be very similar to the present form (e.g. fig. 2).

There is a certain resemblance between the outer whorl of *Nothostephanus kurdistanensis* and that of *Proniceras jimulcense* Imlay from the *Substeueroceras* beds of Mexico (1939: 55, pl. xviii, figs. 1–3), a form that almost looks like a less involute development of the same stock. But the resemblance is believed to be entirely superficial and confined to the outer whorls. The direction of the constrictions alone is sufficient to distinguish the two stocks and the typical *Proniceras* early whorls of the Mexican form confirm the fundamental difference. The derivation of the Tithonian *Proniceras* from the Lower Kimmeridgian *Idoceras* (Burckhardt, 1921, and Djanélidzé, 1922*a*) is based on a similar superficial resemblance.

Four examples in the collection, varying from 15 to 50 mm. in diameter, might be considered to belong to a finely ribbed variety of the present species. They have the small umbilicus of *Nothostephanus*, but unfortunately they are all crushed so as to resemble *Kossmatia* in the outer whorl. Only the primary ribs in all these forms are quite different from those of *K. richteri* Oppel sp. (see Mazenot, 1939: pl. xxi, fig. 4); nor can they be taken to be transitions to *Phanerostephanus*, for the inner whorls are merely young *N. kurdistanensis*, more densely ribbed than the original of Plate 7, fig. 2.

Family OLCOSTEPHANIDAE Kilian, emend. Spath, 1924

Sub-family SPITICERATINAE Spath, 1925

Genus *PRONICERAS* Burckhardt, 1919

Proniceras garaense sp. nov.

PLATE 10, FIGS. 1–3

As holotype of this new species may be taken the example (No. C.40742) figured in Plate 10, figs. 1*a*, *b*, which has the following proportions:

Diameter . . .	59 mm.
Height of last whorl .	25% of the diameter
Thickness of last whorl .	25% ,, ,,
Width of umbilicus .	54% ,, ,,

The whorl-section is almost galeate, as in some *Spiticeras* or in *P. pronum* Oppel sp. (in Zittel, 1868: pl. xv, fig. 8), owing to the high umbilical slope and the small yet distinctly elevated tubercles at the edges. But the early Perisphinctoid whorls are more rounded and the innermost volutions are even depressed, as in the less slowly coiled young *P. toucasi* Retowski sp. figured by Djanélidzé (1922*a*: 64, pl. ii, figs. 1*a*, *b*). The ribbing is similar to that of the form just cited to a diameter of 23 mm. where there is a constriction. The number of these constrictions on the inner whorls is first three then four, but on the outer whorl, which is all body-chamber, there are five. They are greatly projected on the periphery and truncate four or five ribs, the last of which forms an acute chevron on the venter. There is a very long terminal rostrum, projecting 16 mm. beyond the anterior edge of the final constriction.

After the constriction at 33 mm. diameter the primary ribs which seem to be gradually becoming more distantly spaced are developing umbilical swellings. These are conspicuous in the peripheral view but are not actual spines. The ventral sulcus is distinct at the beginning of the outer whorl but then disappears.

The last two suture-lines are visible just before the fracture at the beginning of the outer whorl and they differ from those figured by Djanélidzé (1922) in having the lateral saddle as broad as the external. In their simple outline the elements are comparable to those of the suture-line of *P. minimum* (Jacob MS.) Djanélidzé (1922*a*: 81, text-fig. 15), but the wide, bifid lateral saddle of the present form is at least as indented as the external saddle of *P. minimum*. The short and high second lateral lobe is already at the umbilical tubercle and there is only one more comparatively broad, second lateral saddle on the umbilical slope. It is not impossible that the last suture-lines owe their simplicity to reduction, observed in the final septal edges of many adult ammonites.

A smaller paratype (Plate 10, fig. 2) retains the depressed inner whorls to a later stage than the holotype, so that the whorl-thickness is greater than the height even just before the end of the outer whorl. The aperture is intact, though the ventral lappet is broken off and it is slightly crushed. In spite of various slight differences, however, such as the more clearly marked furrow on the venter of the first half of the outer whorl, this second example and the holotype evidently belong to the same species. The whole of the outer whorl appears to be body-chamber, but the suture-lines could not be exposed.

A third and still smaller example, figured in Plate 10, fig. 3, at first sight also looks like an inflated variety of the present species since its whorl-thickness (36 per cent. at 37 mm. diameter) exceeds the whorl-height (30 per cent.) and since it has a smaller umbilicus (48 per cent.). But apart from the faintness of the ribbing which may be due entirely to slight corrosion, this third example is really indistinguishable from the inner whorls of the holotype at the same size. Unfortunately the suture-line is not visible and the black, bituminous test together with the brown crystalline calcite-matrix does not yield to treatment with acid; but the example seems to be entirely septate.

The periphery of a large fourth example (No. C.41052) with two constrictions has no ventral sulcus. It is only a fragment of a body-chamber, too incomplete to be figured, but it shows that the holotype does not represent the maximum in size. The costation is still regular at what appears to be the apertural end (the second constriction), whereas in both holotype and paratype the ribbing is rather irregular towards the end of the shell.

This species is close to *P. subpronum* Burckhardt (1919–21: 48, pl. xvi, figs. 9–15, &c.), especially to the original of figs. 9–11, but it has a distinctly wider umbilicus and more oblique constrictions. The ventral chevrons of the present form are thus considerably more acute than those of any of the Mexican species of *Proniceras* figured by Burckhardt, or, indeed, of the European forms described by Djanélidzé.

Proniceras simile sp. nov.

PLATE 10, FIGS. 4, 5

This form was at first taken to be only a compressed variety of *P. garaense*, but it differs not only in dimensions but in various other features, notably the suture-line, so that it is now described as an independent species. The holotype (No. C.41053) figured in Plate 10, fig. 4, has the following dimensions:

Diameter . . .	40 mm.
Height of last whorl	30% of diameter
Thickness of last whorl	24% ,, ,,
Width of umbilicus .	51% ,, ,,

The whorl-section is ovate, with flattened sides and an evenly rounded venter. The Perisphinctoid stage is far less pronounced than in *P. garaense*. The innermost whorls are almost smooth to a diameter of approximately 6 mm. and the very strongly projected ribbing remains faint to about 15 mm. After that the primary costae are slightly more distantly spaced but the curvature becomes crescentic (projected at the umbilical end as well as on the periphery). The umbilical nodes are not conspicuous until after the constriction about a quarter of a whorl from the present end of the specimen which itself is at a constriction, the fifth on the outer whorl (entirely septate). The suture-line has a simple trifid lateral lobe and a small lateral saddle, unlike the corresponding element in *P. garaense*. The simple second lateral saddle, as in *P. minimum* (Jacob MS.), above cited, is already on the umbilical slope.

The smaller example figured in Plate 10, fig. 5, is curiously malformed in having a peripheral hump comparable to, but much smaller than, that of *Oecoptychius refractus* (Reinecke). This hump is situated half-way between two constrictions and appears to be perfectly symmetrical when viewed ventrally; but slight displacement of the lateral ribbing suggests that it was due to an injury and therefore pathological.

A large specimen of perhaps 70 mm. diameter has the outer whorl (body-chamber) crushed and appears to be almost smooth; the indistinct umbilical nodes, however, and the secondary ribs of the venter are still visible, in spite of the flattening. Apart from the fact that the peripheral ribs are far more oblique, this large example shows considerable resemblance to *P. neohispanicum* Burckhardt, or at least to the outer whorls of the two specimens figured by that author (1921: pl. xv, figs. 1, 5–7). The 'Idoceratid' inner whorls of the Mexican species, on the other hand, are quite different from those of the form here described.

P. minimum (Jacob MS.) Djanélidzé, already referred to, has faint ribbing, like the present species, but not on the earlier, Perisphinctoid whorls. Its constrictions are also far less oblique and the whorl-section is more rounded.

Proniceras sp. nov. ? ind.

PLATE 10, FIGS. 6*a*, *b*

One apparently new form, represented only by a single specimen, is more coarsely ribbed than the two species described above, and there are no single ribs as in *P. pronum* itself. At least, Zittel's original smaller figures (1868: pl. xv, figs. 9*a–c*, 11*a*, *b*) are no more comparable to the present form than is the lectotype (fig. 8) or the large example (fig. 10) which was excluded from *P. pronum* already by Djanélidzé. On the other hand, one of the fragments included by the latter author in *P. toucasi* (Retowski) var. *dorsosulcata* Djanélidzé (1922*a*: pl. iv, figs. 3*a*, *b*) has similar ribbing, at least on the venter, with its slight, median groove; but the inner whorls of figs. 1 and 2 of the same variety are still much too finely costate.

In the present form the ribs are irregularly bifurcate and trifurcate and almost straight, although the four constrictions are very oblique. On the very broad venter all the secondary ribs have a median sinus, pointing forwards, and there is no suspicion of a tubercle at the point of bifurcation, as in the somewhat similar young forms described above as *Nannostephanus*.

On account of the coarseness of the ribbing and the distinctive appearance of the present form, so different from the typical Mexican species of *Proniceras*, it might even be doubted whether it is correctly interpreted as the inner whorls of a *Proniceras*. The suture-line is not visible, but since the last fifth of the outer whorl is crushed and apparently formed part of the body-chamber, the shell must have been larger than about 33 mm. diameter. The peripheral aspect and the oblique constrictions certainly suggest reference to *Proniceras*. But the general '*colubrinus*'-habit indicates perhaps where the typical *Proniceras* ancestor is to be found. It would also explain the curious resemblance to those transitions between *Nothostephanus* and *Nannostephanus*, referred to on p. 114.

Family PROTANCYLOCERATIDAE Breistroffer, 1947

This family at present includes only the type-genus itself, here represented by the typical *P. kurdistanense*; a new genus of which the genotype, *Cochlocrioceras turriculatum* nov., is described below; and the genus *Bochianites* P. Lory, 1898. There is probably another new genus mentioned above (p. 97) from a bed in the Jebel Gara sequence which is still of Tithonian age. The forms so far described have been referred to such diverse groups as *Crioceras*, *Aegocrioceras*, *Leptoceras*, *Ancyloceras*, *Ptychoceras*, and *Hamites*, while Stoliczka's *Anisoceras gerardi* was redescribed by Uhlig as a form of *Bochianites*. There are thus probably still other genera to be separated in the present family, as and when the forms become known in more detail. But they are clearly not connected with the Neocomian family Crioceratidae, as I understand it. The latter probably originated independently in the Lytoceratidae, whereas Protancyloceratidae were hitherto presumed to be indirect descendants of a Perisphinctoid stock.

As the most probable parent-family of *Protancyloceras* itself I designated the Simoceratidae (Spath, 1939: 581). They are not only the immediate forerunners of *Protancyloceras* in time, being Lower Tithonian, whereas the present family first appeared in the Middle Tithonian, but they include a number of polygyral types such as have repeatedly given rise to uncoiled stocks. In 1925, however, I had already suggested that at least one Simoceratid, namely, *Lytogyroceras* (= group of *Simoceras lytogyrus* Zittel), had a Lytoceratid origin. The costation first appearing on the inner whorls instead of the outer, it had been assumed that *Lytogyroceras* was derived from the Perisphinctidae. Likewise the uncoiling would have affected first the unstable early whorls, following on the protoconch and the first volution (to at least the initial constriction) which rarely uncoils (Plate 8, fig. 4). Now it does not seem to me a coincidence that the long-lived *Protetragonites*, the presumed ancestor of *Lytogyroceras*, was one of the commonest ammonites throughout the Tithonian when Protancyloceratidae arose. There is a close parallel to this appearance of uncoiled derivatives in the Upper Bajocian, where *Spiroceras* and its allies were (probably in error) believed to have resulted from the uncoiling of some polygyral member of the family Parkinsonidae. The astonishing abundance of another Lytoceratid (*Polystomiceras tripartitum* Raspail sp.) during the Parkinsonian age in the Mediterranean area suggests that *Spiroceras* also had a Lytoceratid origin, which indeed has long been accepted for nearly all the numerous heteromorphs of the Cretaceous. The appearance of ribbing in the offshoots of the originally smooth Lytoceratidae would be connected with the change in the mode of life and the ornamentation in its turn may have affected the suture-line.

There are, however, certain exceptions; for example, the genus *Distoloceras* Hyatt is referred to the family Neocomitidae, in spite of the uncoiling of some species. I should also add that one of the new, uncoiled species from the higher beds of Jebel Gara, referred to on p. 97, seems to be connected with the associated Berriasellidae and is apparently not a derivative of *Protancyloceras*. It will, of course, have to be excluded from the present family.

The sub-family Bochianitinae Spath, 1922, is now taken to include the straight end-forms of Protancyloceratidae. I formerly had them as a sub-family in Berriasellidae and Neocomitidae (*not* Parahoplitidae, as Mazenot states); but in 1930 (p. 155) already I suspected the possible connexion of *Bochianites* with the Tithonian genus *Protancyloceras*. The Spiti Shales *Bochianites gerardi*, already mentioned, is one of the transitional forms.

When describing the fauna of the Viñales Limestone of Cuba, R. W. Imlay (1942) was struck with the richness in form and number of uncoiled ammonites which contrasted markedly with the scarcity of such heteromorphs in Tithonian deposits of other parts of the world. Imlay, however, considered the family relationship of his uncoiled ammonites as highly uncertain and he provisionally referred them partly to *Leptoceras*? (family Ancyloceratidae) and partly to *Hamulina*? and *Ptychoceras*? (family Lytoceratidae). The resemblance in shape of the Cuban forms to the Cretaceous genera just mentioned is almost certainly fortuitous and the two species described as *Leptoceras*? *catalinense* and *L.*? *hondense* Imlay are in my opinion typical *Protancyloceras*, comparable to some forms described below as *P.* aff. *gracile* (Oppel) and with similar initial whorls. *Hamulina*? *rosariensis* Imlay probably also falls within *Protancyloceras*, in spite of its final crozier, but whether *Ptychoceras* (?) sp. represents a modification sufficiently distinct for generic separation it is impossible to say in the present state of our knowledge.

Genus *PROTANCYLOCERAS* Spath, 1924

Protancyloceras kurdistanense sp. nov.

PLATE 9, FIGS. 1–5

The holotype (fig. 1) consists of nearly three-quarters of a plane spiral, about half of which is body-chamber and the rest air-chambers. The last septal surface is shown at the fracture, immediately before the change in ornamentation sets in; but apart from the fact that the septal edge is perfectly symmetrical and the lobe-formula is ELUI, i.e. primitive, as in other uncoiled forms, the details of the suture-line could not be made out.

The early whorls are unknown. At the smaller end the holotype has a thickness of nearly 8 mm. where the height is 10 mm. and the whorl-section is oval, slightly wider on the dorsal side than on the ventral. There is a faint, smooth band along the median line of the periphery and a corresponding impressed dorsal area on the opposite side. Later, height and thickness become more nearly equal, and at the end they are both 20 mm. With the change in the ribbing the ventral band becomes a pronounced groove at the end and the dorsal impressed area has disappeared, at least on the test.

The ribbing at first is closely spaced, curved, and strongly inclined forwards, with the costae terminating at the side of the smooth ventral zone but connected across the sulcate dorsum by extremely fine striation. This is straight at first, but becomes increasingly projected forwards so that at the end the strong lateral ribs and the intervening fine lines of growth give rise to dorsal striation that has a flat but pronounced sinus directed forwards. The change in ribbing is already indicated by irregularities just before the last septum, but a few intermediate ribs remain at first on the body-chamber, and even the sixth rib from the end still shows an abortive attempt at splitting up into two. Apart from their general irregularity it is noticeable that the strong ribs are also becoming increasingly projected forwards at the dorsal end. The body-chamber is complete, but the aperture itself is damaged, at least on the figured side. The ventral lappet projects 10 mm. beyond the last rib shown and is evenly and rather narrowly rounded. The last few ribs are not so regularly opposite one another on the venter as the ribs on the earlier part of the body-chamber.

A second specimen (Plate 9, fig. 2), almost as complete as the holotype, has no peripheral groove and the costae of the septate stage are coarser and less closely spaced. These differences are not considered of specific importance, but two more body-chamber fragments (figs. 3, 4) also have no ventral sulcus. There are also two impressions of the finely ribbed septate stage, one of them figured in Plate 9, fig. 5; unfortunately it lacks the beginning of the shell. This was probably similar to the initial whorls described below under *P.* aff. *gracile* or to those of *Hamites* and possibly equally irregular (see Spath, 1939: 605).

There are two more fragments of septate whorls, corresponding to the chambered portion of the holotype, but these also do not show the suture-line.

The genotype of the genus *Protancyloceras*, namely, *P. guembeli* Oppel sp. (in Zittel, 1870: 115, pl. xii, figs. 1–2), is known only in two body-chamber fragments, one of them deformed; but it can be seen at once that the coarse ribs are distantly spaced, short and not curved, except at the beginning of the malformed smaller example. The agreement in the ventral sulcus, the lappet of the aperture, and the dorsal striation, however, makes it probable that the two species belong to the same group.

The *Crioceras* sp. ind. figured by Burckhardt (1919–1921: 58, pl. xxi, fig. 3) from beds with *Parodontoceras* (presumably at the base of the Berriasian) is somewhat like the chambered portion of the species under consideration, but it is too poorly preserved for more detailed comparison. The Mexican *Aegocrioceras* sp. figured by Imlay (1939: 57, pl. xi, figs. 1–2) has coarser and less inclined ribbing than the septate part of *P. kurdistanense*. It may well be a distinct species, and it is interesting because it was also associated with *Proniceras*, but in the *Substeueroceras* Beds.

Protancyloceras sp. aff. **gracile** (Oppel)

PLATE 6, FIGS. 13, 14; PLATE 8, FIG. 4; PLATE 9, FIGS. 6, 8

Cf. 1870. *Ancyloceras gracile* Oppel: Zittel, p. 115, pl. xii, fig. 3.

There are a number of examples of *Protancyloceras* with a general resemblance to Oppel's species, but it is possible that they belong to more than one form and that *P. catalinense* and *P. hondense* (Imlay) are among these. It is not certain, of course, that *P. gracile* had finely ribbed, open whorls in the young. Retowski's (1893: pl. xiv, fig. 5) small fragment, in any case, is not much like any Kurdistan example, and it is straight while still closely ribbed. If correctly interpreted, the Crimean form and Oppel's original must have formed part of much more open spirals, as nearly straight as the large shaft figured in Plate 9, fig. 6. But such changes in coiling need not be of fundamental importance.

The original of Plate 9, fig. 8, may be taken as a typical small fragment of the present form, but the isolated portions of the finely ribbed earlier half of the coil are scarcely visible in the photograph. It is possible to identify with this first example the two fragments of spirals represented in Plate 8, fig. 4. Associated with these on the same piece of limestone are the protoconch, initial whorl, and first part of the uncoiled stage of what is almost certainly the same form, though the slab also contains a fragment of the ubiquitous heteromorph described below as *Cochlocrioceras turriculatum* nov. This protoconch and early stage are missing in Plate 9, fig. 8, but if the original of Plate 9, fig. 6, really represents the final shaft of the same form as the other fragments just mentioned, the species would be fairly completely known as regards shape.

The ribbing in this first form is very gently curved, laterally, and it is distinctly projected ventrally, where it shows its maximum development, except for the pronounced siphonal interruption. It is weaker on the dorsal side, but continuous across, as in Oppel's species. The suture-line is not seen in any of the specimens, but presumably of the simple IULE pattern. Since the suture-line of *P. gracile* is also unknown, the comparison is limited to the external features.

The Jebel Gara specimens so far discussed and provisionally attached to *P. gracile* could also be compared with *P. hondense* Imlay (1942: pl. x, fig. 7). This seems to differ chiefly in its more rigid costation, less distinct ventral interruption of the ribs, and perhaps mode of coiling, though the last character is not here considered of even specific importance.

The originals of Plate 6, figs. 13, 14, and other specimens from a different locality are crushed and this may account for an apparently more rapid rate of increase of the spiral, compared with the solid whorls of the Jebel Gara specimens. The crushed examples just mentioned are more like Imlay's *P. catalinense* (1942: pl. x, fig. 4) with closer ribbing in the early stages and a different rate of increase from *P. hondense*. In view of the fragmentary state of the material available, however, it is not considered advisable to split the forms up into distinct species and I am provisionally attaching them all to the Mediterranean *P. gracile* rather than to Cuban forms that may turn out to be perhaps more distinct than the figures suggest.

Genus ***COCHLOCRIOCERAS*** gen. nov.

GENOTYPE: *C. turriculatum* sp. nov., Plate 8, fig. 8.

DIAGNOSIS: Protancyloceratid with helicoid or turrilitoid early whorls and Ancyloceratid body-chamber, the latter almost in one plane. Ribbing fine at first, but comparatively coarse and distant later, inclined forwards and curved, with a helicoid twist and distinct ventral interruption. Ribs tending to unite in ventral chevrons towards the aperture which is provided with a lappet, as in *Protancyloceras*. Suture-line unknown.

REMARKS: This genus is separated from *Protancyloceras* on the basis of coiling alone, scarcely sufficient in my opinion, though the helicoid twist in the ribbing is likely to have affected even the suture-line. The separation is, however, in conformity with the reference to very diverse but unrelated Cretaceous genera of the different Upper Jurassic uncoiled forms so far described.

The initial whorls (with the protoconch) of a heteromorph, figured in Plate 6, fig. 11, may belong to the present genus. They are associated on the same slab with a typical fragment of *C. turriculatum*, but the initial whorls do not differ from those of *Protancyloceras* (Plate 8, fig. 4) except that they just become uncoiled, without going off in a slender and elongated shaft. Definite identification is perhaps impossible, but it is probable that the earliest whorls in the two genera were similar until they lost contact and went off in different directions, those of the present genus opening out only slightly but becoming helicoid.

Cochlocrioceras turriculatum sp. nov.

PLATE 6, FIG. 11; PLATE 8, FIGS. 4, 8, 9

The most complete example is that figured in Plate 8, fig. 8 (here selected as the holotype), and it shows the impression of at least part of the early helicoid spiral and the Ancyloceratid final shaft, with the terminal but modified portion of the body-chamber preserved in the solid. The complete aperture meets the early spiral almost, but not quite, in the same plane. Length of the body-chamber and suture-line unknown.

The ribbing is fine on the second whorl and there is no slender and elongated, almost straight stage, following on the protoconch and smooth first whorl, as in *Protancyloceras* cf. *gracile* (Plate 8, fig. 4). Instead, the whorls merely lose contact and become helicoid, and where the spiral is about 3 mm. across there are some 24 to 30 fine ribs to the half-whorl, with the twist noticeable already at that stage. Unfortunately, among the many fragments there is not one that shows the change from the fine ribbing following the smooth stage to the coarse costation characteristic of the later whorls; but the ribs are distantly spaced and robust already when the helicoid spiral is only 6 mm. in diameter. The number of ribs then decreases from about 12 to 9–10 to the half-whorl, where it is 8–10 mm. The early whorls (Plate 6, fig. 11) are apparently less turreted than the later stage illustrated in Plate 8, fig. 9*b*, but the originals of fig. 4 (right-hand lower figure) and fig. 9*a* (lower specimen) and numerous other fragments are less extreme and merely helicoid.

The whorl-section is roughly circular, as in *Protancyloceras gracile*; where the whorl-height is 7 mm. (at the end) the thickness is slightly less. The ribs at first are radial and only show the helicoid twist, but towards the final portion they become modified and inclined forwards. They are then slightly curved and the ventral interruption disappears, the ribs forming a chevron on the periphery with the apex pointing forwards. The ventral lappet of the aperture is similar to that of *Protancyloceras guembeli* (Oppel) and *P. kurdistanense*, above described. Just before the aperture the ventral ribbing is rather irregular, compared with the more equally spaced and straighter early costation.

A large number of fragments of the present form were discovered in the matrix of other ammonites, e.g. *Phanerostephanus*, *Nothostephanus*, *Pseudolissoceras*, and the micromorph *Nannostephanus* which is equally common. The fragments are easily recognized by the twist in the ribbing and the rapid increase in curvature; they are much too stout to be confused with the early Leptoceratid stage of the very finely ribbed *Protancyloceras*. There may be a distinct sinus, directed forwards, on the ribs of the venter, but the siphonal interruption of the costae, though present, cannot always be clearly seen in the crystalline, bituminous matrix.

IV. THE AGE OF THE FAUNA

The fauna described in the preceding pages consists of the following nineteen species:

Oxylenticeras lepidum sp. nov.
Glochiceras (?) sp. juv. ind.
Glochiceras (?) sp. nov.
Pseudolissoceras zitteli (Burckhardt)
Pseudolissoceras advena sp. nov.
Lamellaptychus sp. ind.
Phanerostephanus subsenex sp. nov.
Phanerostephanus hudsoni sp. nov.
Phanerostephanus intermedius sp. nov.
Phanerostephanus dalmasiformis sp. nov.
Nannostephanus subcornutus sp. nov.
Nannostephanus sp. ind.
Nothostephanus kurdistanensis sp. nov.
Proniceras garaense sp. nov.
Proniceras simile sp. nov.
Proniceras sp. nov. ? ind.
Protancyloceras kurdistanense sp. nov.
Protancyloceras sp. aff. *gracile* (Oppel)
Cochlocrioceras turriculatum sp. nov.

To these may be added several varieties and related forms, referred to in the descriptions but not named separately on account of defective preservation; also *Virgatosimoceras* sp. nov. ind., which was received after completion of this paper. Although only a body-chamber fragment, it is almost certainly entirely new.

Altogether then there are 20 species (over 200 specimens), no fewer than 16 of them new, and only *Pseudolissoceras zitteli* and *Protancyloceras* aff. *gracile* are attached to known forms, whilst *Glochiceras* (?) sp. juv. and *Lamellaptychus* sp. ind. belong to long-lived, rather indifferent types of little stratigraphical importance. *Pseudolissoceras zitteli* is probably the most valuable of all the forms for dating the fauna, especially as it occurred together with the two distinctive genera *Proniceras* and *Protancyloceras*. It is a species of the Middle Tithonian of Argentina and has more recently been recorded from the approximately equivalent Viñales Limestone of Cuba (Imlay, 1942), where it is also associated with abundant forms of *Protancyloceras*. Some of these, like one of the Kurdistan species, can be compared to *P. gracile* (Oppel), a form of the 'older' Tithonian of Zittel.

This last term must not be confused with what is called the Lower Tithonian stage in the following pages. It denotes rather a miscellany of fragmentary and often condensed deposits, generally highly metamorphosed, or marmorized, ranging from the Upper Kimmeridgian to possibly high up in the Upper Jurassic; for the Rogoznik Breccia, for example, one of the best-known deposits of this 'older' Tithonian, was said to include also a number of forms characteristic of the Upper Tithonian Stramberg Limestone.

These classical, if disconnected, deposits give a very inadequate idea of the duration of Tithonian time, so that before discussing the exact age of the fauna here described it seems advisable to consider the more recent interpretations given to the Tithonian stage. In the absence of unequivocal type-successions which exist for the Kimmeridgian and Portlandian stages, the extent of the Tithonian is still matter of controversy; and the correlation of the freshwater Purbeck Formation or the supposed boreal Volgian with the marine Tithonian remains problematical. In the circumstances I may summarize my own change of view as follows.

When in 1913 I spoke of the '*Acanthicus* Beds' as including both the Upper Kimmeridgian and the Lower Tithonian, I visualized the former as corresponding to Haug's (1909: 1088) zone of *Oppelia lithographica* and the latter to his zone of *Perisphinctes contiguus*, the identity of the Lower Tithonian with the Portlandian being accepted by almost everybody without question. This left Haug's third zone, namely, the zone of *Berriasella privasensis*, as the equivalent of the Upper Tithonian. With Buckman (1922: 6–7) I soon realized, however, that this was far too simple a sub-division of the Upper Jurassic. In tables published in 1923 (p. 304) and 1924 (p. 20) I therefore intercalated the Portlandian between the Tithonian and the Kimmeridgian and lowered the position of the *steraspis* (or *lithographica*) zone, thus increasing the number of zones from three to nine. But, like Buckman and others, I still accepted Pavlow's (1896) and Salfeld's (1914) correlation of the Lower Volgian *Virgatites* beds with the Upper Kimmeridge Clay. It was not until I had worked out for myself the ammonite succession in the Kimmeridge Clay and the Portland Sands (1936: 162–3) and failed to find any true Virgatitids that I suspected that we had wrongly placed the Volgian below the Portlandian instead of above. At the same time it may be admitted that '*Provirgatites*', which precedes the true *Virgatites* in Russia, could be of Portlandian age; but the inner whorls of *Progalbanites albani* (Arkell) I figured from the Portland Sands (Spath, 1936: pl. xx, fig. 2; pl. xxiii, fig. 2; pl. xxiv. fig. 2) bear little resemblance to the restoration of that form published, as '*Provirgatites*', by Arkell (1947: 77, fig. 17, 2). I have not changed my opinion that neither *Provirgatites* nor the true *Virgatites* has yet been found in England.

In any case, I then also expressed the opinion that the distinctness of the fauna of the Rjasan beds from that of the Portland Stone suggested that there was room between them for far more than merely the *virgatus* beds and the Upper Volgian. One of the divisions I then had in mind and found unaccounted for was the whole of Buckman's somewhat problematical 'Proniceratan Age'. I also pointed out that there was no reason why the term Tithonian should not be used for all the beds of the uppermost Jurassic, i.e. all the marine post-Portlandian deposits, boreal as well as Mediterranean. But the real extent of the Tithonian remained uncertain.

From Mazenot's more recent work (1939) it appears that the late Professor W. Kilian made some errors in identifying certain French and other Mediterranean species and that, for example, *Berriasella privasensis*, which most authors had hitherto taken to characterize the topmost zone of the Jurassic, is commoner in the lowest Cretaceous than in the zone that bears its name. I am not in a position to dispute that, but I notice that Mazenot himself lists *Berriasella* 'of the *privasensis* group' from his Lower Tithonian, far below the old *privasensis* zone. Again, that author held that the position of the two sub-zones in the *privasensis* zone should be reversed, i.e. that the *chaperi* and *delphinensis* sub-zones, as adopted from Kilian on previous occasions (e.g. Spath, 1933: 864), are in the wrong order.

I am quite willing to accept a new name for the old *privasensis* zone, if necessary on account of the long range of that species, and I am meanwhile using the more or less equivalent terms *chaperi* and *delphinensis* in Mazenot's sense. But I am sceptical concerning the same author's interpretation of the earlier beds in the Tithonian and consider it quite illogical to include in the Lower Tithonian the *lithographica* zone, as Mazenot does. It is now known to be of Middle Kimmeridgian age, includes such typical genera as *Gravesia* and *Hybonoticeras* (= '*Waagenia*'), and cannot possibly be referred to the (presumably post-Portlandian) Tithonian stage.

Mazenot assumed a gap at the base of the old '*privasensis* zone' in the French Mediterranean succession and thought that the Berriasellids existing during this period were intermediate between those of the Chomérac fauna above and the Neuburg assemblage below. I may here put in a strong objection to the term Palaehoplitidae used by Mazenot for these and other ammonites; it is a pseudo-family name adopted from Roman (1938); it has no legal standing as a systematic unit; and it is meaningless as a popular term. In any case, Mazenot figured examples of certain species, e.g. '*Berriasella*' *subcalisto* and '*Neocomites*' *beneckei*, from both the Chomérac- (Upper) and the St. Concors- (Lower) Tithonian which does not speak in favour of a large gap. Unfortunately the examples of *N. beneckei* figured by Mazenot do not seem to belong to the same species. The typical Upper Tithonian forms (fig. 9) are rather involute and the ribbing shows low branches as in the young *Substeueroceras koeneni* (Steuer), whereas the St. Concors example (fig. 8) has ribs with short branches and a comparatively open umbilicus. Neither of the French forms is identical with Steuer's *Parodontoceras beneckei* which according to Gerth (1925) and Burckhardt (1930) belongs to the zone of *Spiticeras acutum*.

Similarly '*Berriasella*' *ciliata* (Schneid), the index-fossil of Mazenot's upper half of his Lower Tithonian (or '*contiguus*-zone'), is said to persist in the Upper Tithonian *chaperi* sub-zone and to range up into the Cretaceous (Berriasian). This is far too long a range for a specialized ammonite, not belonging to the stable, smooth families, such as the long-lived *Ptychophylloceras ptychoicum* or *Haploceras elimatum*. Moreover, it is not explained why '*B.*' *ciliata* was taken as index-ammonite of a horizon in the lower half of the Tithonian if it persists into the Cretaceous.

Schneid's Neuburg ammonites are difficult to place, as various authors, including myself, have discovered. They may have misled Blanchet (1923) when recording Neuburg species from St. Concors as well as from the presumed equivalent assemblage of Rochefort, near Grenoble; for I certainly cannot see much resemblance between Schneid's constricted 'Pseudovirgatitids' and the unconstricted Berriasellids figured by Mazenot, who accepted Blanchet's identification of the St. Concors and Rochefort faunas with that of Neuburg.

The latter, i.e. Schneid's so-called '*ciliata*-fauna', I have always considered to include a mixture of forms from different horizons, though in 1935 I stated that it did not comprise any pre-Portlandian types. This I had believed probable at first (1925) on the strength of the extraordinary resemblance of some of Schneid's ammonites (*Perisphinctes constrictor*, *P. caesposus*, pars, pl. xii, fig. 3) to *Pallasiceras* and *Pectinatites* of the Upper Kimmeridge Clay, and that view may still be correct. I pointed out at the same time that the Neuburg fauna did not contain a single Tithonian element in the STRICT sense, i.e. any ammonites from the true Upper Tithonian. I am ready now to accept the main Neuburg fauna as falling within the post-Portlandian Jurassic, though not the Upper Tithonian, as claimed by Schneid; but considering that these Neuburg ammonites came from a thickness of beds of over 130 ft. and that they are separated from the underlying Solnhofen beds (*steraspis* zone) by some 330 ft. of limestones and shales with undescribed ammonites, I am still doubtful whether the assemblage described by Schneid can be spoken of as a uniform '*ciliata*-fauna'. In any case, the ammonites from St. Concors figured by Mazenot as '*Berriasella*' aff. *praecox*, '*B.*' *pergrata*, and '*B.*' *adeps* do not appear to me to agree with Schneid's Neuburg originals (my *Parapallasiceras*) nor to be related to those curious *Anavirgatites* and *Pseudovirgatites* that give such a special stamp to the Neuburg fauna. Some of these I described (1925, 1935) from as far afield as British Somaliland, and *Anavirgatites* also occurs in Chile, where a form (*Anavirgatites* **baylei** nom. nov. for *Amm. bifurcatus* Bayle & Coquand, *non* Schlotheim, 1851: 20, pl. ii, fig. 2) was described many years ago, but like other Chilean biplicate ammonites remained unnoticed. The *Anavirgatites* fauna of Somaliland, in the Daghani Section (Spath, 1935: 206), is some 700 ft. higher than Middle Kimmeridgian ammonites (*Streblites*, *Hybonoticeras*), which hardly agrees with Mazenot's placing of these forms (of the *lithographica* zone) in the same lower half of the Tithonian.

The six beds of the *Diphya*-Limestone of Le Pouzin, with '*Perisphinctes*' *contiguus*, and conceivably other deposits, e.g. *Aptychus* beds and limestones with nothing more representative than the long-lived *Phylloceras*, *Lytoceras*, or *Haploceras*, no doubt come within the large gap between the restricted Neuburg fauna and the Middle Kimmeridgian *lithographica* zone, but the fact, stressed by Mazenot, that there are many Perisphinctids is not of much significance. For it may be remembered that there are over 200 ft. of beds with *contiguus*-like ammonites in the Upper Kimmeridge Clay (my *grandis* and *wheatleyensis* zones, 1936), and these are succeeded by higher Kimmeridgian and Portlandian ammonite faunas teeming with Perisphinctids which represent another 725 ft. of deposits. They are not accounted for in Mazenot's scheme and certainly cannot be included in a true Tithonian. But I am unable to say whether the fauna of Le Pouzin is a strictly homogeneous fauna or even whether it is entirely post-Portlandian, as the abundance of late types like *Kossmatia richteri*, *Semiformiceras fallauxi* (Oppel), &c., suggests.

A correlation of the few zones recognized by Mazenot in the south of France with those given by Burckhardt and Imlay for the Mexican and by Leanza for the Andine Tithonian is attempted in the following table. But this correlation is tentative and is meant to show where the beds of Jebel Gara that yielded the present fauna (and the succeeding assemblages briefly referred to) are believed to come in. Thus I am retaining the older divisions of the *Substeueroceras* beds, simply because several assemblages (with different species) have been collected on Jebel Gara; to recognize only one *koeneni* zone, as Leanza does, might give a misleading picture. Then the name *tenuistriata* zone, dating from 1923, is used for the *Kossmatia* beds, instead of *pseudodesmidoptycha* zone (Krantz, 1926; Burckhardt, 1930); for that Andine species with tuberculate inner whorls seems to be widely different from the true Indian *tenuistriata* group.

The genus *Kossmatia* is still imperfectly understood. Mazenot (1939) considered his '*Berriasella*' *richteri* (Oppel) to range from the Lower Tithonian into the Cretaceous, which is obviously impossible. In fact, the true *Kossmatia richteri*, refigured by Mazenot, is quite different from the Rogoznik *Perisphinctes richteri* figured by Zittel (1870: pl. xxxiii, fig. 4 only). This has the graceful ribbing and small umbilicus of *Grayiceras* and connects directly with *G.* **kiangurense** nom. nov. (for '*Simbirskites*' n. sp. ind. in Uhlig, 1910: 275, pl. lxxxi, fig. 2), which itself leads, by way of another new Spiti species (No. 83939, with wider umbilicus and closer costation) to the typical *Kossmatia*. In this, as in the closely allied *Paraboliceras* Uhlig (connected with *Kossmatia* by *K. desmidoptycha* Uhlig), the ribs, in the nepionic stage only, are blunt and comparatively coarse, bifurcating or single, inclined forwards as a whole, and not at all or at least not appreciably effaced in the siphonal line. Strachey's smaller example of *K. tenuistriata*, badly figured in Salter and Blanford (1865: pl. xv, fig. 2), is another new species of the same group, as is the less umbilicate *K.* **decipiens** nom. nov. (for *K.* n. sp. ind. in Uhlig, 1910: 276, pl. xci, fig. 2), with equally sharp and short secondaries on cast or test. But I am not in a position to say whether the Mexican species of *Kossmatia*, which according to Imlay are larger and more numerous than those of any other country, are as close to the European and Indian forms as that author believes.

There is some uncertainty about the next lower zones of the Upper Tithonian because the identifications of '*Neocomites*' *kayseri* (Steuer) and *Berriasella calistoides* (Behrendsen) adopted as zonal ammonites by Burckhardt (after Krantz) are open to doubt. The former species could be a late form of the *occitanica* group and in any case was associated with higher Tithonian types at La Manga. The other is one of the various controversial border-line species; it was recorded by Weaver from his Upper Tithonian; by Leanza from the higher *Substeueroceras* beds at the top of the Tithonian; Mazenot had it from the lowest Cretaceous of the south of France; and I used *Parodontoceras calistoides* (after Kilian) as an alternative name for the *calisto* zone at the base of the Berriasian.

For the lowest zone, at the base of the Upper Tithonian, I am adopting Leanza's zone of *Windhauseniceras internispinosum* (see p. 131). According to Krantz this form occurred together with such an early type as *Aulacosphinctes colubrinus* (*non* Reinecke), also with *Corongoceras lotenoense*. If *C. alternans* (Gerth) is found to occupy a distinct level above *C. lotenoense* (and *C. mendozanum* of Burckhardt's *calistoides* zone), Leanza's name *alternans* zone is available for the intermediate zone left unnamed in the table below.

The two zones of the Middle Tithonian are adopted from Burckhardt (1930: 112, table 11), but it is doubtful whether these and the few zones of the very incompletely known Lower Tithonian are sufficient to accommodate even the faunas so far described. There are serious objections to the continued use of the term *contiguus* zone for this Lower Tithonian. In 1925 and 1930, when putting this species in the genus *Subplanites*, I took it to be of Upper Kimmeridgian age, though previously

(1923) I had called it a Tithonian *Aulacosphinctoides* and had, in fact, suggested the term 'Aulacosphinctoidan Age' in place of '*contiguus* zone' which was retained merely because it was better known to the general geologist (p. 305). Both views are probably right. Unfortunately the revision of the diverse species that have been included in *Amm. contiguus*, considered desirable already by Uhlig (1910) and Neaverson (1925), is still outstanding. Meanwhile I can only suggest that the resemblance of some forms, e.g. the alleged Stramberg *Perisphinctes* (*Virgatosphinctes*) cf. *contiguus* (Catullo) of Blaschke (1911) to the genus *Virgatosphinctoides* Neaverson of the Upper Kimmeridge Clay, and of others (e.g. Uhlig's) to the associated *Aulacosphinctoides* of the Spiti Shales, is a case of heterochronous homoeomorphy, comparable to that of the Callovian and Argovian '*Macrocephalites*'. There are differences in the suture-lines and in other still less obvious characters, such as the ribbing, constrictions at different stages, &c., perhaps even the appearance in thin, median sections. There is, of course, also the possibility that the alleged horizons of some marmorized ammonites from the Alpine-Mediterranean Tithonian are unreliable.

Apart from the rearrangement of the zones and sub-zones, one important change now made in comparison with previous tables consists of the transfer of the *Virgatites* beds of the Volgian from the Upper Kimmeridgian to the post-Portlandian. The true *Virgatites* fauna (which does not include certain other Volgian ammonites often grouped with it) could be as late as the upper half of the Eo-Tithonian, not necessarily a counterpart of the *ciliata* zone, but probably not higher. This means that Pavlow must have been wrong in correlating with the Portland Stone the sands containing large ammonites that follow on the phosphatic conglomerate with '*Virgatites*'; for those lower beds of the so-called Volgian that succeed the Kimmeridgian *pseudomutabilis* zone and include first *Gravesia* and then *Pectinatites* and *Pavlovia* are clearly a condensed representation of the Upper Kimmeridge Clay and the Portland Sands (see above, pp. 97, 128).

The ammonites figured by Buckman as *Virgatites pallasianus* (d'Orbigny) and *V. scythicus* (Michalski), by Arkell as *Provirgatites*, and by myself as *Progalbanites*, like the East Greenland *Epipallasiceras*, &c., are all forerunners of the true *Virgatites*. I did not realize in 1923 what a mixture of forms of different ages had been included in '*Virgatites*'; and though I mistrusted the Kachpur sequence I gave, on the basis of Blake's collecting, it did show that the *Virgatites* and *Epivirgatites* fauna immediately preceded the Upper Volgian *Craspedites* faunas. The opinion then expressed that the latter might be boreal equivalents of the Tithonian *Proniceras* and *Haploceras*, though now shown to be correct, was unfortunately vitiated by the general belief that Salfeld's researches had settled the age of '*Virgatites*'.

On the other hand, it would be unsafe in the present state of our knowledge to stress the apparent affinity between the presumably later genera *Nothostephanus* and *Phanerostephanus* here described and their Volgian counterparts *Virgatites* and *Epivirgatites* (*nikitini* group) respectively. Altogether, the Virgatitinae (and 'Pseudovirgatitinae') are not now considered to be so fundamentally different from the Virgatosphinctinae, as Uhlig (1910) thought, and there are many passage-forms between the latter and the persistent *pseudocolubrinus* root-stock. Hence they also tend to resemble occasionally some of the genera grouped in the more or less parallel development, the Pavlovinae, until finally the presumed last survivor of the Perisphinctid stock, *Virgatosphinctes transitorius* (Oppel), became extinct in the Neo-Tithonian. It does not differ essentially from its presumable forerunners of the type of *V. pompeckji* Uhlig (1910: 320, pl. lxv, fig. 1); but its ephemeral ventral groove shows that it is already transitional to the rapidly rising Berriasellidae.

The *Craspedites* zones of the Upper Volgian then falling naturally into the Middle Tithonian, correlation is possible between the Russian *Riasanites* and its Andine equivalent, *Corongoceras*, of the lower Neo-Tithonian.

The earlier *Virgatosphinctes* beds of Madagascar, of Kachh, and of the Spiti Shales may all be of slightly different ages and perhaps not one is the exact counterpart of the well-known deposit of Le Pouzin or of the Andine *V. mendozanus* zone of Burckhardt. They are now all provisionally included in the *contiguus* zone or the *pseudocolubrinus* beds (s.l.) of the Lower Tithonian, and therefore considered to be post-Portlandian; for the true Portlandian ammonite fauna, perhaps unknown from any part of the world except southern England and the Boulonnais, is closely connected with that of the Upper Kimmeridge Clay and forms part of the same Pavlovian age. As already mentioned (p. 97), this may link up with the *pseudocolubrinus* beds of the table below, but is widely separated from the Berriasellan age of the Upper Tithonian.

Table of Emended Divisions of the Tithonian

TITHONIAN	Neo-	'privasensis'	chaperi	Substeueroceras beds	permulticostatum	s, t, u
			delphinensis		acutum	
					koeneni	
		'pronus'		Kossmatia and Durangites beds	tenuistriata	
					....	
	Meso-			(?) Pseudolissoceras beds	internispinosum	i
					colubrinoides	
			(gap)		zitteli	
	Eo-	'contiguus'	St. Concors		....	
				Pseudocolubrinus beds	ciliatum	
					....	
			Le Pouzin		Virgatosphinctes	

With regard to the ammonites here described, it may be mentioned that although the great majority came from one bed (*i*) on Jebel Gara, 33 ft. thick, they were not collected inch by inch. At first sight they seem to belong to one uniform assemblage, however, for not only in the matrix of examples of *Pseudolissoceras*, but also in that of various species of *Phanerostephanus* and *Nothostephanus*, and even *Proniceras*, there occur fragments of *Nannostephanus subcornutus* and of *Cochlocrioceras*. These are the two commonest forms in the bed, so that the ammonites are at least largely, if not entirely, from one horizon. The presence of *Pseudolissoceras* suggests a horizon in the Middle Tithonian in which the Berriasellidae, so characteristic of the Upper Tithonian, played as yet a very minor part, while the Perisphinctids, dominant in the Lower Tithonian, were correspondingly more numerous. There is no evidence for considering *Proniceras* to have come from a higher level on Jebel Gara than *Pseudolissoceras*.

A few specimens have been added which are not from Jebel Gara but from another locality to the west (Shiranish Islam, Zakho District). They are apparently from a bed of about the same age, and if left out of this account would not affect the general conclusions. Yet it is interesting to note that though there are several specimens of *Oxylenticeras* and *Protancyloceras* from this second locality, there is no example of either *Nannostephanus subcornutus* or of *Cochlocrioceras turriculatum*, the two commonest ammonoids in the Jebel Gara fauna. *Pseudolissoceras zitteli* is also absent; but there are several complete examples of *P. advena* sp. nov., as already mentioned, in addition to bad impressions that must remain under suspicion because the collection from Shiranish Islam also contains a Lower Kimmeridgian *Sutneria* in a similar preservation (brownish calcite in a black bituminous matrix). Moreover, the ten forms of ammonoids here figured from that locality are either new or else not quite the same as their counterparts in the Jebel Gara fauna. They are:

Plate 6, figs. 3, 5. *Oxylenticeras lepidum* sp. nov., varieties
fig. 7. *Glochiceras* (?) sp. nov.
fig. 10. *Pseudolissoceras advena* sp. nov.
fig. 12. *Nannostephanus* sp. ind.
figs. 13, 14. *Protancyloceras* sp.
Plate 8, fig. 3. *Phanerostephanus intermedius* sp. nov.
fig. 5. *Nannostephanus* (?) sp. ind.
Plate 10, fig. 12. *Lamellaptychus* sp. ind.

The assemblage as a whole is in a less favourable state of preservation than that from Jebel Gara, but there seems to be no doubt that the two faunas are not exactly synchronous. The fact that the second assemblage includes a large example of *Proniceras*, apparently identical with *P. simile* from Jebel Gara, may be taken to indicate that the difference in level is only slight.

The genus *Proniceras* is said to be essentially Upper Tithonian. All the French forms figured by Djanélidzé (1922*a*) are referred to that sub-stage, and they are nearly all from Chomérac (Ardèche) and associated with *Spiticeras*. Imlay (1939) described species from the *Substeueroceras* beds of Mexico, without *Spiticeras*; and while he questioned the correctness of Burckhardt's (1930) placing of his *Proniceras* bed, Imlay insisted that the stratigraphical position of that genus was above that of *Kossmatia* and not below.

That, however, may not be true for all the forms of *Proniceras*. The name *pronum* zone is no longer applicable if *P. pronum* itself is confined to the uppermost (Stramberg) Tithonian. Proniceratan age (Buckman, 1922) seems preferable, but is not really helpful, while the range of the genus *Proniceras* remains unknown, and the same might apply to the Kossmatian Age which I substituted in 1923. But it is possible that *Proniceras* is connected by intermediaries with forerunners like the 'Lower Tithonian' *Pseudosimoceras* (group of *Olcostephanus stenonis* Gemmellaro); for it may be remembered that Kilian (1889) identified this early species with Pictet's *Amm. narbonensis*, a form now included in the very advanced *Spiticeras* (*Kilianiceras*). This connexion would make the affinity between *Proniceras* and the *colubrini* less close than was suggested above (p. 120), but Simoceratidae have been held to be Perisphinctid derivatives, showing the essential similarity of these stocks.

The ammonites of the *Proniceras* bed of Burckhardt (1930: 57, text-figs. 18*a–c*) in any case do not include *Substeueroceras* of the overlying shales. On the contrary, they are associated with species of *Aulacosphinctoides* (one of them transitional to *Micracanthoceras*), comparable to forms of the Spiti Shales and Madagascar which do not appear to be of high Tithonian age. In view of the coexistence in the present fauna of *Proniceras* with *Pseudolissoceras* and the other distinctive genera, but a complete absence of Berriasellidae, also the fact that this fauna came from a bed over 250 ft. below the top of the Jurassic, it might well be considered to be of pre-*Kossmatia* age, if not actually Middle Tithonian, the age of *Pseudolissoceras* in South America. To see this in true perspective, however, it should be remembered that the zone of *Pseudolissoceras zitteli* alone, i.e. Weaver's (1931) Middle Tithonian, in central Neuquen (Vaca Muerta Region), includes some 660 ft. of black shales and limestones out of a total thickness of 2,660 ft. for the Tithonian in Weaver's interpretation, that is WITHOUT the *Substeueroceras* beds. The Kurdistan succession, or at least the fossiliferous portions outlined on p. 97, therefore probably includes only disconnected fragments of the Upper Tithonian, with the new fauna here described from bed *i* at its base.

There is a possibility that the Kurdistan species of *Pseudolissoceras* are not isochronous with the Andine *P. zitteli*, and that in spite of a smaller umbilicus they are closer to the Carpathian *P. planiusculum* (Zittel), although this also is a form of the 'older' Tithonian and has not been found at Stramberg. To what has been said on p. 102 I can only add that the differences are very slight and that all the species of *Pseudolissoceras* may well come from one horizon. The coexistence of that genus with typical *Simoceras* (*volanense* group) in the Argentine Andes and in Cuba as well as in Europe makes it probable that it is not of high Tithonian age.

Another possibility is that the fauna from bed *j*, a 48-ft. bed of black shale, overlying bed *i* (which yielded the ammonites here described), is already of high Upper Tithonian age, in spite of its position at over 200 ft. below the top of that stage. The evidence is not conclusive, for half the fauna of bed *j* consists of a form that has the graceful, sigmoidal, lateral ribbing and the small umbilicus of *Grayiceras*, but the ribs are not projected appreciably at the ventral end. All the twenty-five specimens, however, are crushed, and not one shows the periphery. Then there are five specimens of what appears to be *Substeueroceras* ? *striolatum* (Steuer) and one new form, with the inner whorls more finely ribbed than those of *S. koeneni* (Steuer), but the outer whorl considerably more degenerate (in ribbing) than that of the much larger holotype of Steuer's species. There is only one crushed periphery of a typical, large *Substeueroceras*.

Parodontoceras is also represented by only one example, comparable to *P. beneckei* (Steuer), but this must belong to a persistent group, for the ammonite is not very different from a form of the same genus, doubtfully attached to *P. calistoides* (Behrendsen) from bed *s*, about 150 ft. higher in the succession. An impression of a *Spiticeras* with Perisphinctoid inner whorls, resembling *S.* (*Kilianiceras*) *chomeracense* Djanélidzé, could also belong to the zone of *Spiticeras acutum*, like *Parodontoceras beneckei*.

The rest of the Berriasellids (and Perisphinctids ?) of the latest collection from bed *j* are not readily identifiable. They include impressions of several large forms, notably a fragment of a *Substeueroceras* like *S. ellipsostomum* (Steuer) of the *koeneni* zone. Another distantly resembles the fragment figured by Burckhardt (1906: pl. xxxviii, fig. 2) as *Hoplites* cfr. *calisto* Zittel (*sic*), but it has peculiarly flattened ribs. A third form has a diameter of 170 mm. and is apparently undescribed, for I cannot even suggest a genus for it. It has straight, distant costation on the earlier whorls, exposed in the wide umbilicus, but the smooth outer whorl has strong and short secondaries only near the ventral edge. There is no indication of the original appearance of the periphery. I may add that I am not here recording a fair number of recognizable examples of Berriasellids said to have been collected 'from the scree of bed *j*' (old collection) because they may have come down from higher beds.

On the whole, then, the fauna of the bed overlying bed *i* that yielded the ammonites here described lacks the typical Berriasellids of the uppermost Tithonian as well as *Proniceras*. The dominant genus, *Grayiceras*, is known to be associated with *Kossmatia* in Mexico, and it probably occupies the same horizon in the Himalayas where its companion genus is *Paraboliceras*, in place of the Mexican *Durangites*. In other words, bed *j* would probably come within the *tenuistriata* zone of the above table, although three of the species mentioned have been found in the higher *koeneni* and *acutum* zones. But while the beds with *Kossmatia*, *Durangites*, and *Grayiceras* are taken to be of Upper Tithonian age, these ammonites are not associated with any of the late Tithonian forms of *Berriasella* of the *delphinensis* type or of *Protacanthodiscus* (*chaperi* group) described from, for example, Aizy (Isère) or Theodosia in the Crimea. These only occur in the top beds (*t–u*) of Jebel Gara.

If I am right about the stratigraphical position of the ammonites from *j* it may explain the absence of *Kossmatia* from bed *i* below. This, however, has yielded both the presumed later *Proniceras* and the earlier *Pseudolissoceras*, which perhaps indicates that either genus had a longer range than is generally believed. With regard to the first, it must suffice to point out that the Kurdistan species of *Proniceras* are different from those of Mexico or Chomérac (Ardèche). On the other hand, *Pseudolissoceras*, being a Haploceratid, i.e. one of the smooth, fundamental stocks, is more likely to have an extended range than the more specialized and ornamented *Proniceras*. On the whole I am not in favour of assuming long ranges of certain ammonite genera to explain an apparent anomaly, unless there is far more convincing evidence than in the present case. There are as yet too many gaps in the succession and in our knowledge of the Tithonian stage to be dogmatic. Thus it is almost certain that the forms of *Kossmatia* from Imlay's (1943) locality 17252 are widely separated, stratigraphically, from the beds that yielded his *Subplanites* and *Virgatosphinctes* at the same locality, as, indeed, the difference in matrix and preservation had already suggested to Imlay. It may not be out of place in this connexion to emphasize that this fauna from locality 17252 itself occurred hundreds of feet above beds with *Hybonoticeras* ('*Waagenia*') according to the collectors, W. S. Adkins and R. E. King. There is room here yet for other new and unsuspected faunas, as there is in the corresponding gap between the Middle Kimmeridgian and the *Anavirgatites* beds (*ciliatum* zone) of Somaliland, referred to on p. 128.

The Tithonian, in short, is probably as incompletely developed in Mexico as in all the other countries so far explored, including Kurdistan, where there may be no Lower Tithonian at all.

The reader will probably have come to the conclusion that we workers on ammonites uphold the world-wide distribution of these organisms for reasons of convenience and because we would like to be able to determine more or less mechanically the age of a deposit by means of the ammonites. The present account, on the other hand, rather supports what I said in 1933 (p. 794), that it seemed there was indeed no means of exact—as distinct from approximate—parallelization of beds from one continent to another and that the different groups of ammonites did not modify in the same way and at exactly the same rate in the different provinces.

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PLATE 6

Figs. 1–5. *Oxylenticeras lepidum* sp. nov. Side- and peripheral views of holotype (1*a*, *b* = C.41118). Side-view of another example (2*a* = C.41117) with crushed body-chamber and (2*b*) solid septate whorls reversed. Side- and peripheral views of a ribbed variety (3*a*, *b* = C.41119). Peripheral view of a small compressed example (4 = C.41120); and side- and peripheral views of an inflated variety (5*a*, *b* = C.41122). P. 99.

Figs. 6*a*, *b*. *Glochiceras* (?) sp. juv. ind. Side- and peripheral views (C.41107). P. 100.

Fig. 7. *Glochiceras* (?) sp. nov. Terminal portion of body-chamber (C.41106). P. 101.

Figs. 8*a–c*. *Pseudolissoceras zitteli* (Burckhardt). Specimen showing portion of ribbed body-chamber crushed on to septate, smooth whorls (8*a* = C.41115); also side- and peripheral views of another example (8*b*, *c* = C.41116). P. 101.

Figs. 9–10. *Pseudolissoceras advena* sp. nov. Side- and peripheral views of holotype (9*a*, *b* = C.41110) and of a smaller example (9*c*, *d* = C.41109); also side-view of a specimen with narrower venter (10 = C.41186). For suture-line see Plate 8, fig. 10. P. 102.

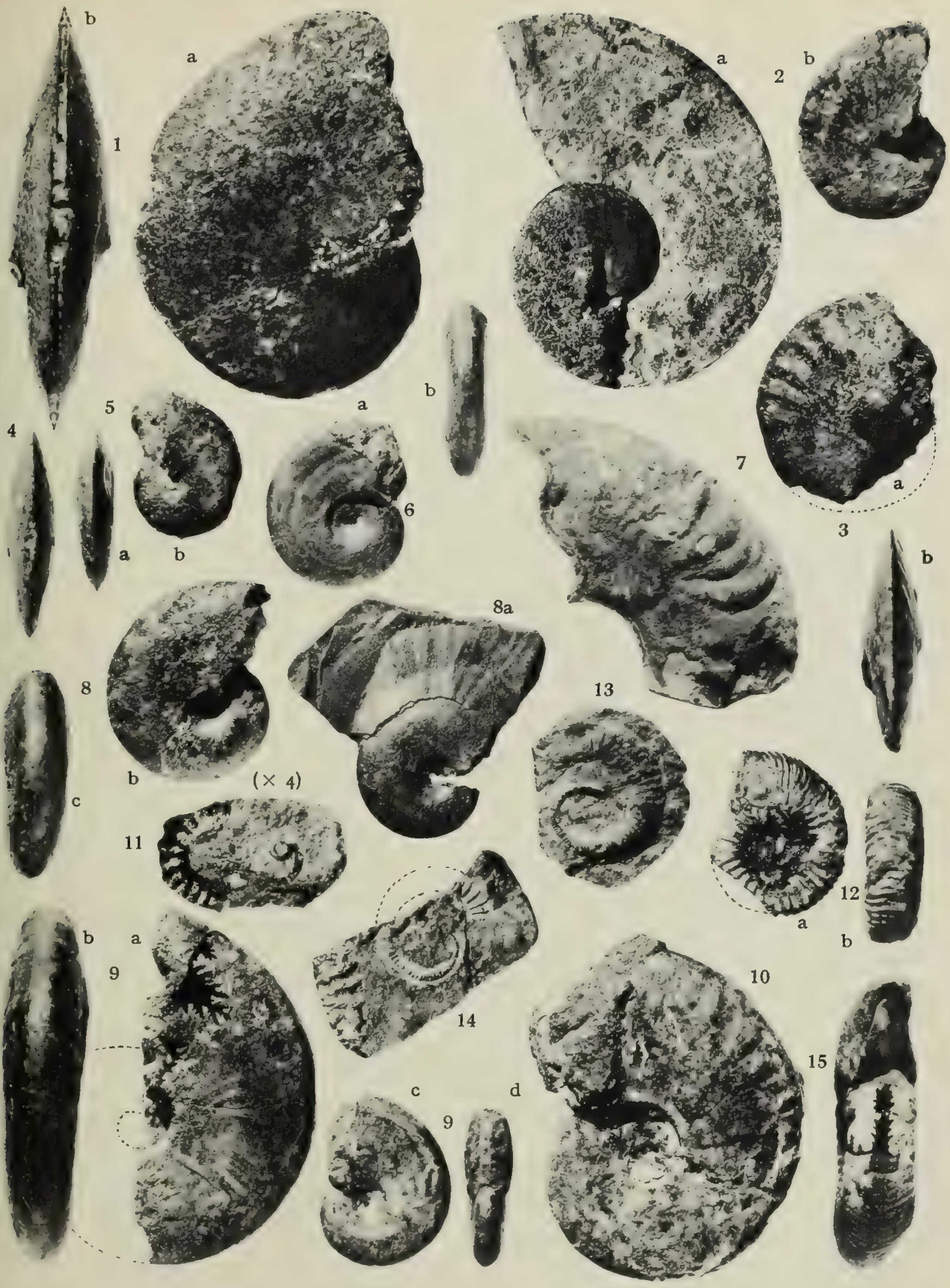
Fig. 11. *Cochlocrioceras turriculatum* sp. nov. Typical fragment (left) and initial whorls and protoconch of same? (enlarged ×4). C.41156. P. 124.

Figs. 12*a*, *b*. *Nannostephanus* sp. ind. Side- and peripheral views (C.41162). P. 111.

Figs. 13, 14. *Protancyloceras* sp. Two crushed specimens (C.41158–41159) with resemblance to *P. catalinense* (Imlay). P. 122.

Fig. 15. *Phanerostephanus subsenex* sp. nov. Peripheral view of the example (C.40744) figured in Plate 7, fig. 6. P. 105.

All the specimens on this plate are from Jebel Gara, near Amadia, Kurdistan, except figs. 3, 5, 7, 10, 12, 13, 14 which are from Shiranish Islam, Zakho District.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TITHONIAN AMMONOIDS FROM KURDISTAN

[illegible]

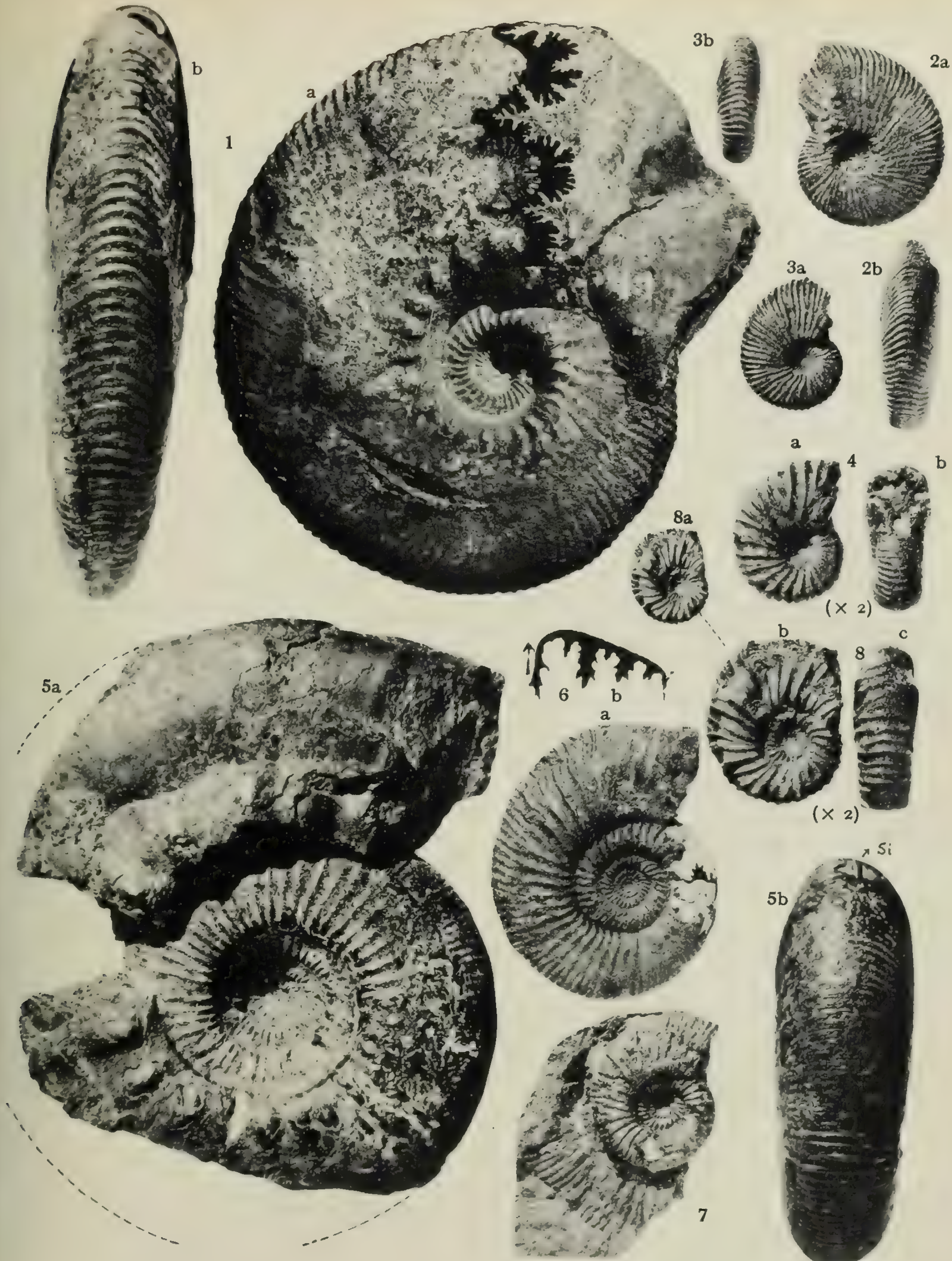
PLATE 7

FIGS. 1–4. *Nothostephanus kurdistanensis* sp. nov. Side- and peripheral views of holotype (1 = C.40745) and three young examples (2 = C.41111; 3 = C.41112; 4 = C.41113). P. 116.

FIGS. 5–7. *Phanerostephanus subsenex* sp. nov. Side-view of holotype (5*a* = C.41166) and peripheral view of its earlier whorls (5*b*); also two smaller examples (6 = C.40744; 7 = C.41184). 6*a* = suture-line, enlarged and restored from fig. 6*a* and the peripheral view in Plate 6, fig. 15. P. 105.

FIG. 8. *Nothostephanus* sp. juv. aff. *kurdistanensis*, sp. nov. transitional to *Nannostephanus*. Side-view (8*a* = C.41114) and side- and peripheral views enlarged × 2 (8*b*, *c*). P. 116.

All the specimens on this plate are from Jebel Gara, near Amadia, Kurdistan.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7

TITHONIAN AMMONOIDS FROM KURDISTAN

[illegible]

PLATE 8

FIGS. 1, 2. *Phanerostephanus hudsoni* sp. nov. Side- and peripheral views of holotype (1*a*, *b* = C.40746) and of a large septate fragment (2*a*, *b* = C.40749). P. 107.

FIGS. 3*a*, *b*. *Phanerostephanus intermedius* sp. nov. Side- and peripheral views of septate whorls of holotype (C.41130). Impression of outer whorl omitted. Shiranish Islam, Zakho District. P. 107.

FIGS. 4*a*, *b*. *Protancyloceras* sp. aff. *gracile* (Oppel). Slab with portions (left) of two larger examples and early whorls with protoconch (top, right); also fragment of *Cochlocrioceras turriculatum* sp. nov. (bottom, right). C.41155. P. 122.

FIGS. 5*a–c*. *Nannostephanus* (?) sp. ind. Side- and peripheral views of a doubtful young specimen (C.41129); also side-view enlarged ×2. Shiranish Islam, Zakho District. P. 111.

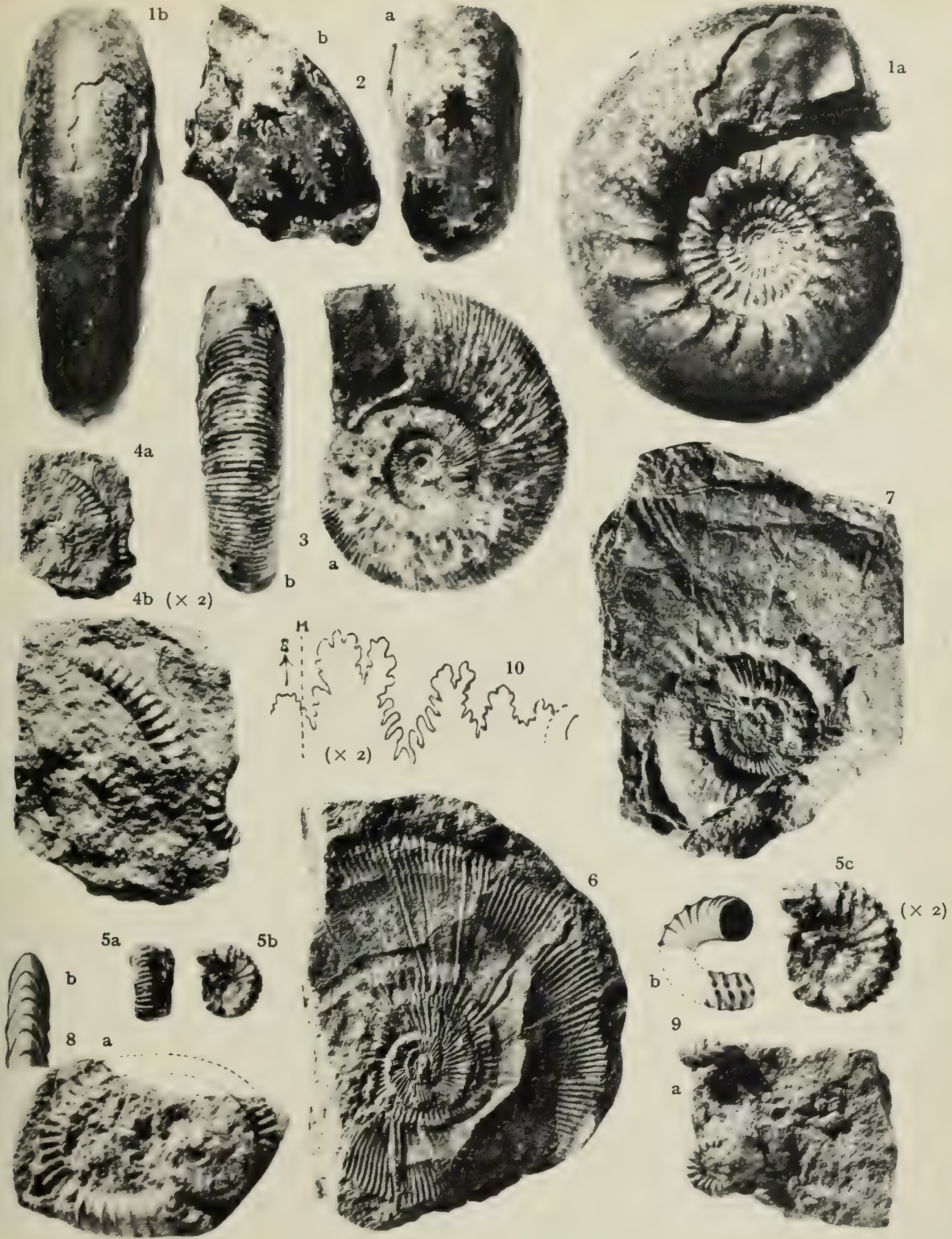
FIG. 6. *Phanerostephanus* cf. *intermedius* sp. nov. Doubtful crushed specimen (C.41131). P. 107.

FIG. 7. *Phanerostephanus dalmasiformis* sp. nov. Crushed holotype (C.41164). P. 109.

FIGS. 8, 9. *Cochlocrioceras turriculatum* sp. nov. Holotype, with portion of periphery near aperture (8*a*, *b* = C.41157) and paratype, with outline of top-left fragment, restored and enlarged from impression in rock (9*a*, *b* = C.41153). P. 124.

FIG. 10. *Pseudolissoceras advena* sp. nov. Asymmetrical suture-line, enlarged ×2, of a small example (? variety without umbilical edge) from Shiranish Islam, Zakho District (C.41187). P. 102.

All the specimens on this plate, except figs. 3, 5, and 10, are from Jebel Gara, near Amadia, Kurdistan.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TITHONIAN AMMONOIDS FROM KURDISTAN

[illegible]

PLATE 9

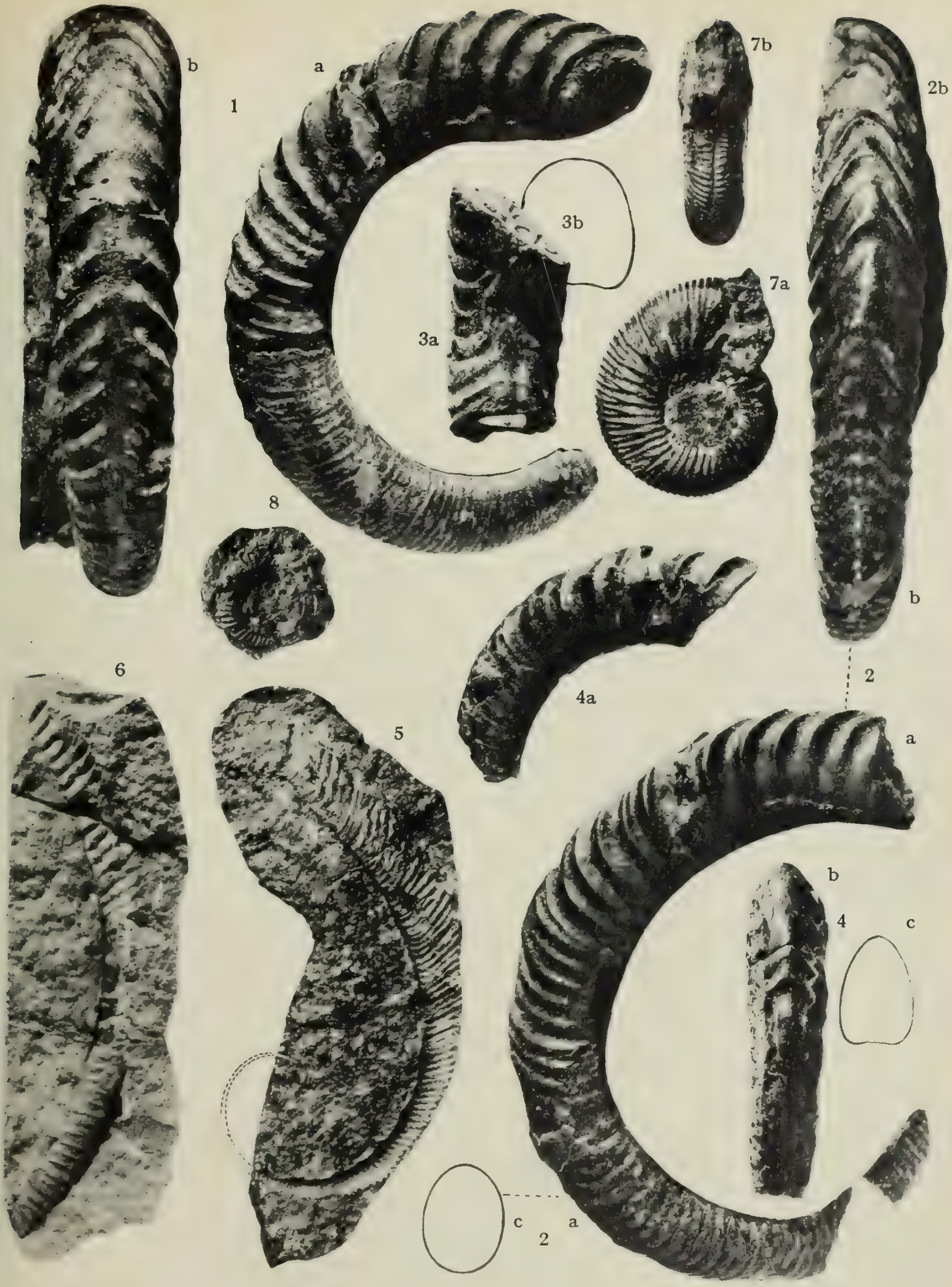
FIGS. 1–5. *Protancyloceras kurdistanense* sp. nov. Side- and peripheral views with outline whorl-section of holotype (1*a*, *b* = C.40743), and paratype (2*a*–*c* = C.41057); dorsal view and outline whorl-section (3*a*, *b* = C.41058) and lateral and ventral views and whorl-section (4*a*–*c* = C.41059) of two body-chamber fragments, also impression of septate portion of another example (5 = C.41060). P. 121.

FIG. 6. *Protancyloceras* sp. aff. *gracile* (Oppel). Impression of largest example (C.41160). P. 122.

FIGS. 7*a*, *b*. *Phanerostephanus* sp. ind. nov.? Side- and peripheral views of a small, doubtful example, with ventral groove (C.41185). P. 106.

FIG. 8. *Protancyloceras* sp. aff. *gracile* (Oppel). Early whorl (C. 41154). Note finely ribbed portion on right. P. 122.

All the specimens on this plate are from Jebel Gara, near Amadia, Kurdistan.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TITHONIAN AMMONOIDS FROM KURDISTAN

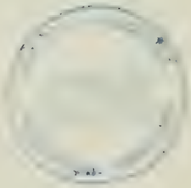


PLATE 10

Figs. 1–3. *Proniceras garaense* sp. nov. Side- and peripheral views of holotype (1*a*, *b* = C.40742) and paratype (2*a*, *b* = C.41050), also of a smaller example (3*a*, *b* = C.41051). P. 117.

Figs. 4, 5. *Proniceras simile* sp. nov. Side- and peripheral views of holotype (4*a*, *b* = C.41053) and of a malformed smaller example (5*a*, *b* = C.41054). P. 118.

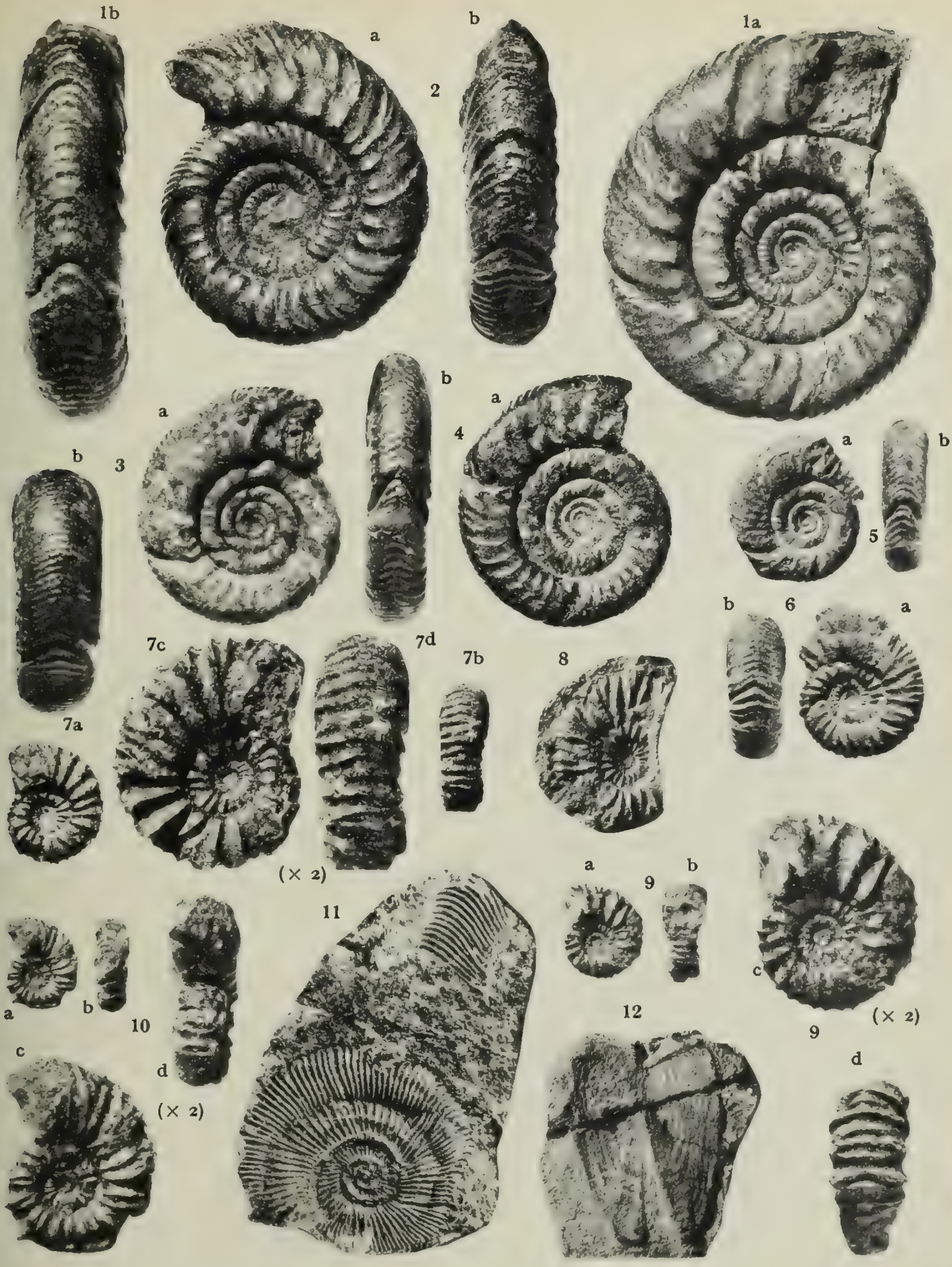
Figs. 6*a*, *b*. *Proniceras* sp. nov.? ind. Side- and peripheral views (C.41056). P. 119.

Figs. 7–10. *Nannostephanus subcornutus* sp. nov. Side- and peripheral views, natural size and enlarged × 2 of holotype (7*a*–*d* = C.41066) and of two paratypes (9*a*–*d* = C.41065; 10*a*–*d* = C.41067); also squeeze of a doubtful impression (8 = C.41075). P. 111.

Fig. 11. *Phanerostephanus* sp. ind. Doubtful impression (C.41161) perhaps of *P. intermedius* sp. nov., with portion of venter of another individual. P. 107.

Fig. 12. *Lamellaptychus* sp. ind. Showing concave side (C.41105). Shiranish Islam, Zakho District. P. 104.

All the specimens on this plate, except fig. 12, are from Jebel Gara, near Amadia, Kurdistan.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PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

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BRITISH MUSEUM NATURAL HISTORY

T. H. WITHERS

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THOMAS H. WITHERS

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Pp. 147–170; *Pls.* 11–14; 6 *Text-figures*

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CRETACEOUS AND EOCENE PEDUNCLES OF THE CIRRIPEDE *EUSCALPELLUM*

By THOMAS H. WITHERS

(*With Plates* 11–14)

SYNOPSIS

Some curious fossils have been known since 1871 from the Upper Cretaceous of South Island, New Zealand, but it has not been possible to define their systematic position. They are now shown, with others from the Upper Cretaceous of Graham Land and the ? Upper Eocene of Tierra del Fuego, to be monstrously developed peduncles of a Cirripede. The occurrence of similar peduncles associated in the same beds with capitular valves in the Eocene of U.S.A. shows that they belong to the genus *Euscalpellum* Hoek, a genus so far unrecognized among fossils.

INTRODUCTION

So long ago as 1871 Haast collected some unusual fossils from the Cretaceous of Waipara Gorge, N. Canterbury, New Zealand. Of these he said (1871: 45):

> 'In the thick greensand strata overlying the Septaria clays in the Waipara, I obtained some fossil shells which appear to be allied to Radiolites, the occurrence of which may therefore point to an upper cretaceous age. This important fact in connection with the occurrence of the few fossils before enumerated, compels me to modify my views concerning the age of the Waipara beds, always supposing that the Radiolites-looking bodies belong to that genus of extinct cretaceous conchifera.'

Many years later Dr. J. Allan Thomson collected further specimens and said (1920: 346):

> 'Fossils are very scarce in the Waipara greensands, the most common being an obscure form from the lower group which has defied recognition. They consist of calcareous tubes, ½ in. to 1 in. in diameter and a few inches in length, the interior being filled with matrix. Von Haast (1871B) recorded the presence of "some shells which appear to be allied to Radiolites" and the specimens he collected are preserved in the Geological Survey collections. They resemble the calcareous tubes collected by me, but are distinguished by the presence of nodal-like marks at intervals, giving the specimens an external resemblance to an equisete stem. Dr. Marie Stopes, who kindly examined the series of specimens, writes that they are certainly not Equisetinean or structures of any higher plant, and that Professor Garwood, who also carefully examined them, concluded that they were not algal; she showed them also to specialists working on lowly animals, but none of them would claim them, and the consensus of opinion was that they were inorganic.'

Recently (March 1950) three series of specimens of this New Zealand fossil from the Waipara Gorge have been presented to the Geological Department of the British Museum, namely: (1) eighteen incomplete specimens which Mr. C. W. Weston brought to this country for identification, some coming from precisely the same locality from which Allan Thomson collected his specimens, and others from two points near by; (2) six specimens and two slides from Dr. Marie C. Stopes originally forming part of the material collected by Dr. Allan Thomson and sent to her by him; (3) three specimens, much more complete than the others, collected by Dr. C. T. Trechmann: these were exhibited by Dr. Trechmann at a meeting of the Geological Society of London (1950: 86) as a 'problem fossil'.

On examining these specimens Mr. W. N. Croft of the Geological Department observed that they were similar to some specimens he had collected in Graham Land, already determined by me as peduncles of a Cirripede. On this, Mr. W. N. Edwards, Keeper of the Geological Department, sent all the material (twenty-seven specimens) to me for examination, and they were readily recognized as monstrously developed peduncles of a Cirripede, *Euscalpellum*, far exceeding in length and solidity anything as yet discovered among stalked Cirripedes. This recognition was possible because a species, *Euscalpellum eocenense* (Meyer), here referred to that genus for the first time, occurs in the Middle Eocene of Mississippi and Texas, and the capitular valves occur together in the same bed with remains of a comparatively strongly plated peduncle, and this gave a clue to the remaining forms. The form of the capitular valves of *E. eocenense* leaves no doubt at all that this species is congeneric with the genotype of *Euscalpellum*, the Recent *E. rostratum* (Darwin), of which the holotype came from the Philippine Archipelago (20 fathoms).

I wish to thank Mr. W. N. Edwards for kindly taking so much trouble in looking up the New Zealand references and for his kind help; Dr. J. P. Harding for kindly making drawings of the holotype of *Euscalpellum rostratum*; Prof. H. B. Stenzel of Texas University for assistance and for sending material of *E. eocenense*; Miss W. McGlamery of Alabama Geological Survey for material of *E. eocenense*; Dr. Katherine Van Winkel Palmer, and the Standard Oil Co. of New Jersey, for the opportunity of describing the specimen of *E. crassissimum*; and the Falkland Islands Dependencies Survey for the opportunity of describing the material from Graham Land.

PEDUNCLES

The peduncle of the Middle Eocene *E. eocenense* (Meyer) from Mississippi (Pl. 13, figs. 13, 14) is thick and strong, and the plates are close-set. Each plate is formed of a solid oblong block of calcite directed obliquely downwards (Pl. 13, fig. 13*b*). The inner ends of the plates are of irregular shape and are flattened to form the sides of the small median or sub-median canal, and the outer ends form the outer face of the peduncle and are there developed into an upturned projecting finger-like process. The largest piece of peduncle has a length of 27·3 mm. and a breadth at the top of 9·7 mm. Certain of the capitular valves in this species show decided signs of thickening.

Another peduncle, *E. crassissimum* n.sp. (Pl. 14, figs. 1–5) from the ? Upper Eocene of Tierra del Fuego, has an incomplete length of 104·0 mm., breadth 30·0 mm., and where broken obliquely across near the top of the peduncle, 66·0 mm. This is a massive peduncle having a superficial resemblance to a pine-cone. Except that the plates are much larger than in *E. eocenense*, and the outer ends not finger-like, but flatly rounded and mostly wider than, or as wide as, high, the resemblance is unmistakable. One individual plate has an inner extension of 7·5 mm., and the height of the outer face is about 5·0 mm.

The Antarctic form, *E. antarcticum* n.sp. (Pl. 12, figs. 2–4) from the Upper Cretaceous (Upper Senonian) of Graham Land, is represented by five incomplete peduncles, collected by Mr. W. N. Croft in 1946 when serving as a geologist in the Falkland Islands Dependencies Survey. These are comparatively thick and massive, and, except in one specimen (Pl. 12, fig. 4), the plates are disposed as in *E. eocenense* and *E. crassissimum*, but the outer ends of the plates have a different shape, for they are generally more elongated and taper towards the rounded apex.

Had it not been for the peduncle of *E. eocenense*, and those from Tierra del Fuego and Graham Land, in which they are formed entirely of separate plates, it might have been difficult to place the curiously developed peduncles from the Upper Cretaceous of New Zealand (*E. zelandicum*, Pl. 11, figs. 1–3; Pl. 12, fig. 1). The outstanding features of these New Zealand peduncles are their very strong curvature, their narrowness and length (the largest has a length of 115·0 mm. and along the outer curve, 195·0 mm.), their solidity, and the plates not being developed in the upper part of the peduncle. More curious still, where the plates are developed there is no sign where the peduncle is broken across, or in the transverse sections, of plates extending inwards towards the median canal, such as are seen in the peduncles of *E. eocenense*, *E. crassissimum*, and *E. antarcticum*. It is evident that in *E. zelandicum* the projecting plates near the base are in an erect position, and except for these the peduncle is solid as far as the sub-median canal. Maybe the plates have become completely fused in the body of the peduncle. The upper comparatively smooth part of the peduncle has transverse, often wavy, and irregularly prominent growth-bands, recalling superficially a shell of the Rudist *Radiolites*. Anything less like Cirripede peduncles it would be difficult to imagine, but in fact that is what they are.

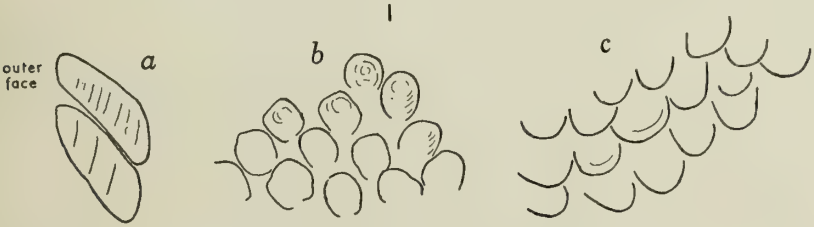


FIG. 1. *Euscalpellum rostratum* (Darwin). Recent. Holotype.
a, side view of two plates of peduncle; *b*, outer face of several plates; *c*, inner ends of several plates. × 43 diam.

The holotype of the Recent *Euscalpellum rostratum* (Darwin) is a very small form having a total length of 9·3 mm., length of capitulum 6·3 mm., and peduncle, 3·0 mm.

Darwin (1851: 260) said in his description: '*Peduncle*, short, about half the length of the capitulum; narrow; thickly clothed with minute, longitudinally elongated, spindle-shaped, calcareous scales or beads, which project but little.' Dr. J. P. Harding of the Zoological Department, British Museum (Natural History), most kindly made for me some camera lucida drawings of part of the peduncle of the holotype, and from these (Fig. 1*a*) it is clear that the plates, although so minute, agree in their elongated form with those of the fossil species. In *E. eocenense* the outer end of each plate is produced into a projecting finger-like process; in *E. antarcticum* the outer end of each plate is produced into a comparatively wide projecting plate which increases rapidly in width downwards; but in *E. rostratum* the outer ends of the plates are flattened to form longitudinally oval beads (Fig. 1*b*) which project but little. The inner ends of the plates (Fig. 1*c*) in *E. rostratum* are rather like overlapping tiles, and they are not so irregular in shape or so compacted as in *E. eocenense*.

CAPITULAR VALVES

Unfortunately the capitular valves are known only in *E. eocenense*, so that those of the other species are still to be found. *E. zelandicum* occurs in the Waipara Greensand in hundreds, and it is therefore curious that no capitular valves could be found among so many peduncles. It would be interesting to find the capitular valves of *E. zelandicum*; they would be comparatively small in comparison with the length of the peduncle, for the size of these valves usually bears some relation to the width of the peduncle at the top, and as this is only 24·0 mm. in the largest peduncle, the capitular valves could not be more than twice the size of the largest valves of *E. eocenense*.

It is quite unusual to found Cirripede species on peduncles, but in view of the great interest of these extraordinary forms, and the fact that it is possible to differentiate between them, little can be advanced against it in this instance.

DISTRIBUTION

The fossil species here described under the genus *Euscalpellum* add considerably to our knowledge of the geological and geographical distribution of that genus, and so far no fossil species has been referred to it.

There are six Recent species, namely:

E. rostratum (Darwin). Indian Ocean; South Arabian Coast, Mergui Archipelago; Malay Archipelago (15–113 metres, on Hydroids and horny corals). Nilsson-Cantell, 1938: 2.

E. bengalense (Annandale). Indian Ocean (125–925 metres), on crabs, and a few individuals on horny corals at great depths.

E. renei (Gruvel). Saint-Paul de Loanda, Angola (on Hydroid).

E. squamosum Hiro. Off Tonda, Kii Channel, Wakayama Pref., Japan (190 metres, on Hydroid).

E. squamuliferum (Wettner). Indian Ocean; Malay Archipelago. On *Hyalonema* (101–3,475 metres).

E. stratum (Aurivillius). Antilles Sea (360–680 metres).

None of these species occurs north of latitude 40° N. or south of latitude 40° S. We now know that species occurred in the Upper Cretaceous of Graham Land and South Island, New Zealand, in the ? Upper Eocene of Tierra del Fuego, and in the Middle Eocene of the U.S.A. An undescribed form is known to me by capitular valves from the Miocene of Cuba; one from the Miocene of Australia; and *Scalpellum* (? *Arcoscalpellum*) *meridianum* Chapman & Crespin (1928: 131, pl. x, fig 72) from the Miocene of Australia, is obviously also a species of *Euscalpellum*. In Europe *E. minutum* (T. Brown) occurs commonly in the Lower Eocene (Ypresian) London Clay of England and *E. vomer* (Bertrand) in the Middle Eocene (Lutetian) of France and England. Other unpublished species are known to me from the Eocene of England and Italy, and plates too imperfect for description from the Upper Miocene of Czechoslovakia. Altogether there are thirteen fossil species known to me (some not yet described), ranging from Upper Cretaceous to Miocene, so the genus not only had a long range but a wide one in geological times.

According to a photograph supplied by Dr. Trechmann, the New Zealand species *Euscalpellum zelandicum* occurs in hundreds in the Waipara Gorge, forming almost a Cirripede-bed at that particular spot. In a letter from Professor R. S. Allan he writes:

> 'Some years ago I rediscovered the locality in the Middle Waipara Gorge whence Thomson and probably von Haast had originally found this fossil. Here however specimens are comparatively rare. In 1948–49 one of my honours students, J. C. Schofield, M.Sc., discovered a new locality in the Upper Waipara District, at which it occurs in great abundance. I have since collected a wealth of well preserved material.'

It is therefore curious that this species is not known elsewhere in the New Zealand Cretaceous, for one would expect it to have a wider range. The genus is also unknown in beds above the Cretaceous in New Zealand, although it is represented in the Miocene of Australia.

Dr. Trechmann's photograph does not suggest that the Cirripedes were preserved in their position of growth, for they are scattered irregularly in the matrix. If the heavy peduncles accumulated after the death of the animal to form a kind of shell-bank, the absence of the much lighter capitular valves might be due to differential sorting, and in that case it might be worth while hunting for the missing valves in adjacent beds on the same horizon, if these can be traced, as well as in the 'cirripede banks' themselves.

ECOLOGY

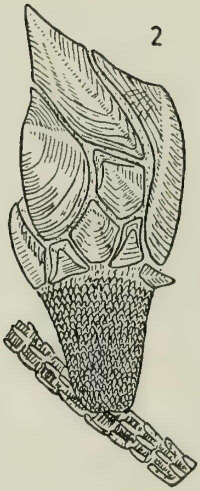
One problem is what gave rise at different times to the development of such heavy peduncles. With such strongly curved and heavy peduncles they could hardly have been attached to crabs and hydroids, but one or two specimens suggest that they had been attached to some object. It may be that this was an adaptation to living on a sandy or muddy bottom, perhaps influenced to some extent by wave or current action, and in consequence of this there was a need for increased weight or anchor. A change in the conditions could easily lead to their extinction, and these particular forms appear to have died out, and more normal species are known fossil from Eocene to Miocene.

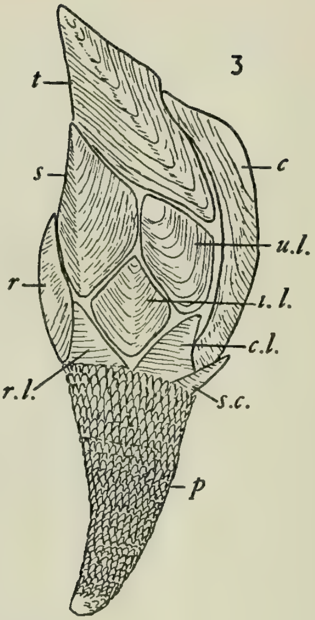
It can hardly be a case of the mere piling up of calcium carbonate due to the excess of this in the water (see Withers, 1935: 8), for these forms all occur either in sand, shale, or marl, with glauconite.

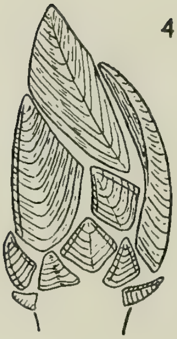
PHYLOGENY

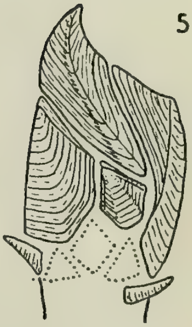
The geologically earliest species of *Euscalpellum* with monstrously developed peduncles are *E. zelandicum* and *E. antarcticum* from the Upper Cretaceous. As *E. zelandicum* has no plates developed on its upper half, it has gone farther along the road to solidity than *E. antarcticum* from the Upper Cretaceous (Upper Senonian) of Graham Land. Although the peduncle of *E. eocenense* from the Middle Eocene (Claiborne group) of U.S.A. is strongly plated, it is not so monstrously developed as in the two former species.

Among the Eocene and later species of *Euscalpellum* there is a definite trend in the capitular valves towards the removal of the umbo from the apex owing to the upward growth of the valves. This development occurs independently in different species and









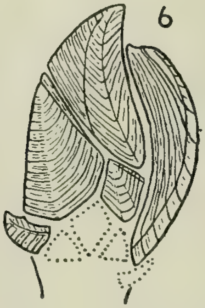


Fig. 2. *Euscalpellum rostratum* (Darwin). Genotype. ×6 diam. Recent: Philippine Archipelago (20 fathoms). (After Darwin.)

Fig. 3. *Euscalpellum squamosum* Hiro. ×7·5 diam. Recent: Japan (Pacific Ocean side; 190 metres). (After Hiro, now Utinomi.)

Reconstruction of Capitula.

Fig. 4. *Euscalpellum minutum* (Brown). ×2 diam. Lower Eocene, Ypresian, London Clay: England.

Fig. 5. *Euscalpellum vomer* (Bertrand). ×3 diam. Middle Eocene, Lutetian, Calcaire Grossier: France (Paris Basin).

Fig. 6. *Euscalpellum eocenense* (Meyer). ⅔ nat. size. Middle Eocene, Claiborne group: U.S.A.

(*c*, carina; *c.l.*, carinal latus; *i.l.*, infra-median latus; *r*, rostrum; *r.l.*, rostral latus; *s*, scutum; *s.c.*, sub-carina; *t*, tergum; *u.l.*, upper latus.)

affects different valves; but some species remain conservative and have the umbo apical in all valves.

The earliest of the Eocene species is *Euscalpellum minutum* (Brown; Fig. 4), from the Lower Eocene (Ypresian) of England, and this has the umbo of all valves apical. *E. vomer* (Bertrand; Fig. 5), from the Middle Eocene (Lutetian) of France and England, is a more advanced form, for the carina, scutum, and upper latus have the umbo removed from the apex, although in the latter valve this development has only just appeared. *E. eocenense* (Meyer; Fig. 6), from the Middle Eocene (Claiborne group) of U.S.A., has the carina and scutum slightly removed from the apex, but the upper latus still has an apical umbo.

Miocene species like *E. meridianum* (Chapman & Crespin) from Australia are conservative species for the umbo of all valves remains apical.

Among the Recent species, *E. stratum* (Aurivillius), *E. bengalense* (Annandale), *E. squamuliferum* (Weltner), and *E. squamosum* Hiro (Fig. 3), have the umbo of all valves apical; but in the genotype, *E. rostratum* (Darwin; Fig. 2), the valves attain their highest development, for not only has the umbo in the carina, scutum, and upper latus a sub-apical position, but so has the umbo in the basal latera, and a similar development to this is seen in *E. renei* (Gruvel). All the Recent species are small forms, the largest, *E. squamuliferum*, having only a complete length of 38·0 mm. (capitulum 18·0 mm.; peduncle, 20·0 mm.), and the others less than half that length.

SYSTEMATIC DESCRIPTION

Sub-class *CIRRIPEDIA*

Order THORACICA

Sub-order Lepadomorpha

Genus ***EUSCALPELLUM*** Hoek

Type species *E. rostratum* (Darwin), 1851: 259, pl. vi, fig. 7; Hoek, 1907: 59; by subsequent selection, Pilsbry, 1908: 107. Recent, Philippine Archipelago (20 fathoms).

1. ***Euscalpellum zelandicum*** n.sp.

Plate 11, figs. 1–3; Plate 12, fig. 1

1871 *Radiolites*? Haast, 1871: 45; Thomson, 1920: 346.

Diagnosis. An *Euscalpellum* with the peduncle long, narrow, strongly curved, solid except for a small sub-median canal; plates formed only on the lower part of the peduncle, the upper part more or less smooth, except for the irregular growth-bands. Plates generally twice as high as wide, with the sides square-edged or rounded, and the apical part rounded off. Capitular valves unknown.

Distribution. Upper Cretaceous, Teurian (Upper Senonian), Greensand: Several exposures in the Waipara Gorge, North Canterbury, New Zealand. 'Below the bed of concretions with reptile bones. Two beds standing vertically 10 ft. apart about 150 ft. above the basement greywacke' [Trechmann].

Allan Thomson (1920: 341) included the Waipara Greensand in the Piripauan Stage and regarded this as of Upper Senonian age. Finlay & Marwick (1940: 84) also refer the Waipara Greensand to the Piripauan Stage, with a possible age of Santonian-Campanian, i.e. Middle to Upper Senonian. Later, Finlay & Marwick (1947: 229) included the Waipara Greensand in a new Stage (Teurian) placed above the Piripauan, which is regarded as of Senonian age. The type-locality of the Teurian is the Te Uri stream, and Finlay & Marwick (1947: 230) say: 'No microfauna is known at the type locality; but molluscs and reptile remains are known in the Waipara greensands.' In this passage microfauna is evidently a misprint for macrofauna since there is a good foraminiferal fauna at Te Uri.

HOLOTYPE. A nearly complete peduncle (Pl. 11, fig. 1), collected by Dr. C. T. Trechmann, in the Geological Department of the British Museum, In. 43731.

MATERIAL. In the British Museum (Natural History) there are eighteen incomplete peduncles from Waipara Gorge, collected and presented by Mr. C. W. Weston, March 1950, registered In. 43734–In. 43751.

Two almost complete, and the upper half of another peduncle from the Waipara Gorge, collected and presented by Dr. C. T. Trechmann, March 1950, registered In. 43731–In. 43733.

Six incomplete peduncles and two slides from Waipara Gorge (original Nos. 36, 277, 835), sent by Dr. J. Allan Thomson to Dr. Marie C. Stopes, and presented by her, March 1950. In. 43752–In. 43757.

MEASUREMENTS. Largest peduncle (Pl. 11, fig. 2), length 115·0 mm., along outer curve 195·0 mm., breadth 23·5 mm. The holotype, a nearly complete peduncle (Pl. 11, fig. 1) length 82·5 mm., breadth 20·0 mm. Peduncle, upper half (Pl. 11, fig. 3*a*), length 85·0 mm., breadth 24·0 mm.

DESCRIPTION. Peduncle (Pl. 11, figs. 1–3; Pl. 12, fig. 1) long, narrow, strongly curved, very gradually increasing in width upwards, sub-circular in transverse section at the lower end, broadly oval at the upper end, and solid except for a small sub-median canal. All the specimens are weathered to a greater or lesser extent, but plates are formed only on the lower part of the peduncle. These plates are regularly developed near the base, and do not disappear suddenly above, but occur sporadically towards the top of the lower half or less of the peduncle. The incomplete peduncle (Pl. 12, fig. 1) shows the form of the plates more clearly; they are generally somewhat elongated, about twice as long as wide, with the sides square-edged or rounded, and the apical part rounded off, and they are distinctly projecting. Upper part of peduncle comparatively smooth, with transverse somewhat wavy growth-lines, and unequally prominent growth-bands. At the top of one specimen (Pl. 11, figs. 3*a*, *b*), which appears to be complete at this end, there is a deep depression with rather smooth sides, rather like the alveolar cavity of a Belemnite. The base in the peduncle (Pl. 11, fig. 1) is narrowed off, but this may be due to the fact that it is broken. In this same specimen the joints between the plates are clearly seen on one side at the base, but neither in this nor in other specimens can it be seen that there is a block of calcite extending inwards from the outer face such as is the case with the plates of *Euscalpellum eocenense*, *E. crassissimum*, and *E. antarcticum*. On the contrary, except for the plates seen on the outer surface, the peduncle is completely solid as far inwards as the small submedian canal, and no trace of inwardly extending plates, or of sutures between plates can be seen either in the specimens where broken, or in the transverse sections. Certain of the incomplete peduncles (Pl. 12, fig. 1*b*) appear to have had a flat, broadly oval to circular base, for the joints of the plates are there shown, and in the middle there are remains of a thin calcareous film.

2. ***Euscalpellum antarcticum*** n.sp.

PLATE 12, FIGS. 2–4

DIAGNOSIS. An *Euscalpellum* with the peduncle comparatively wide, showing some curvature; plates developed for its whole length, usually formed of an oblong block of calcite extending inwards to the sub-median canal, close-set, and generally with a small outer face, variable, but often elongated, somewhat rounded transversely, and tapering towards the apex. Capitular valves unknown.

DISTRIBUTION. Upper Cretaceous, Upper Senonian[1] (in glauconitic sandy clays and nodules): The Naze (lat. 63° 55′ S.; long. 57° 30′ W.), and Humps Islet (lat. 63° 59′ S.; long. 57° 25′ W.), NE. Graham Land, Antarctica. A shelly fauna and drifted wood are associated with the Cirripedes.

HOLOTYPE. An incomplete peduncle (Pl. 12, fig. 2) from The Naze (D97.4A), collected by Mr. W. N. Croft, in the Geological Department of the British Museum (Natural History), In. 43813.

MATERIAL. Five incomplete peduncles (The Naze, Nos. D85.7, D86.8, D90.5, D97.4A, from localities on the slopes between Dagger Peak and Comb Ridge; Humps Islet, No. D529.4, from the saddle between the two eminences.) Registered In. 43813–In. 43815; In. 43906–In. 43907. Collected by Mr. W. N. Croft, and presented by the Government of the Falkland Islands 1950.

MEASUREMENTS. Holotype, D97.4A (Pl. 12, fig. 2), length 44·5 mm., breadth 23·7 mm. D85·7 (Pl. 12, fig. 3), length 64·0 mm., breadth 23·8 mm. D86.8 (Pl. 12, fig. 4), length 78·0 mm., breadth 24·2 mm. D90.5, breadth about 45·0 mm. D529.4 is a mere fragment, length 21·5 mm., breadth 16·8 mm.

DESCRIPTION. The peduncles vary in width, but are comparatively wide. There is considerable variation in the shape of the outer faces of the plates, for they vary from as long as wide to three times as long as wide. The plates are somewhat projecting, transversely rounded, taper towards the apex, and the umbo often stands out prominently, as can be well seen in the holotype (Pl. 12, fig. 2). The holotype represents part of a peduncle broken longitudinally down the middle, and shows the solid oblong plates almost horizontally inclined on the left side, and obliquely inclined upwards on the right side; they extend inwards nearly to the median canal which is fairly wide. This is the structure seen in three of the peduncles, and is probably normal.

The longest part of a peduncle (Pl. 12, figs. 4*a*, *b*) is exceedingly curiously developed; it is not known which part of the peduncle it represents, but is possibly the upper part. Outwardly the plates are very much elongated, some are very large, long, and wide, and others long and narrow; in some cases the sutures between the plates are well seen, and in others they do not extend for the whole length of the plate, and certainly give the appearance that some of the plates are incompletely fused together. Looking at the top of this peduncle (Pl. 12, fig. 4*b*) it was thought at first that the plates were of the shape seen in the holotype, that is, they were oblong blocks laid one upon the other. Instead they are the inwardly directed portions of these outer, much elongated and variably shaped plates; they differ markedly in shape, length, and in the degree to which they extend inwards (Pl. 12, fig. 4*b*). This is a somewhat different development from that of the holotype.

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[1] A more precise age determination will be given in a forthcoming work on the associated ammonite fauna by Dr. L. F. Spath.

3. ***Euscalpellum eocenense*** (Meyer)

PLATE 13, FIGS. 1–14

1885 *Scalpellum eocenense* O. Meyer, *Amer. J. Sci.* (3) **30:** 70, figs. *a–c*.
1897 *Scalpellum chamberlaini* Pilsbry, *Proc. Acad. Nat. Sci. Philad.* **1897:** 332, fig. 1.

DIAGNOSIS. An *Euscalpellum* with the carina having the umbo slightly removed from the apex, parietes very wide, extending to the base. Scutum very wide, umbo slightly removed from the apex, the tergal edge produced outwards. Tergum wide, moderately bowed towards carinal side. Upper latus with apical umbo. Rostrum thick and solid, the sides produced upwards. Peduncle cylindrical; plates with the outer extension finger-like.

DISTRIBUTION. Middle Eocene, Claiborne group: Texas to Alabama.

Weches formation: bluff on right bank of Colorado River at Smithville, Bastrop County, Texas (Bureau of Econ. Geology Loc. 11-T-2); Concord–Centerville County road, north ditch, 0·6 mile south-east of Robbins depot, in south corner of J. M. Powell 100-acre tract, in south corner of R. M. Tyus survey, Leon County, Texas (Loc. 145-T-1); Concord–Centerville road, north ditch, 5·2 miles west of courthouse of Centerville, between left tributary of McDaniel Creek and Sparta nose, east part of J. T. Smith 290-acre tract, Jos. Walker survey, Leon County, Texas (Loc. 145-T-38); road ditches at bottom of hill on Grapeland–Dailey road, 8·2 miles west of the railroad at Grapeland by speedometer, G. Greenwood survey, Houston County, Texas (Loc. 113-T-15); Berryman's place, 3 miles north-east of Alto, Cherokee County, Texas.

Wautubbee formation: cut on Alabama and Vicksburg railroad on Indian Mound in pasture of Mr. A. H. Edwards, 3 miles east of Newton, Newton County, and cuts on New Orleans and North-eastern railroad, about 1 mile north of Wautubbee, Clarke County, Mississippi.

Lisbon formation: Coffeeville landing on Tombigbee River, Clarke County, Alabama; old landing on Alabama River at Claiborne, Monroe County, Alabama.

HOLOTYPE. Meyer originally gave figures of three valves, a carina (fig. *a*), and figs. *b*, *c*, which he referred to only as 'lateralia of the same species?', and these 'lateralia' are respectively a scutum (fig. *b*) and rostrum (fig. *c*). The carina must therefore be regarded as the holotype, but the specimen cannot now be identified in the Meyer collection. The scutum and the rostrum are now preserved in the Geological Survey of Alabama. The only description is 'Besides the figured piece *b*, I found valves of the same form but larger. The umbo of the carina is placed at the apex'. This latter, however, is incorrect.

MATERIAL. Eighty-nine specimens (31 carinae, 27 scuta, 12 terga, an upper latus, 6 rostra, parts of 2 peduncles, and 10 peduncle plates), including 9 carinae, 7 scuta, and a rostrum, from Claiborne, Alabama, 10 carinae, 6 scuta, and 3 terga from Wautubbee, Miss., and a scutum from Coffeeville Landing, Tombigbee River, Alabama, all in the Geological Survey of Alabama (Meyer colln.); 6 carinae, 7 scuta, 6 terga, 2 rostra, an upper latus, and 7 peduncle plates, from bluff on right bank of Colorado River, at Smithville, a scutum from east of Robbins road-crossing, a scutum and tergum from west of courthouse at Centerville, 2 rostra from old landing, near Claiborne, parts of two peduncles from Wautubbee, Miss., all in the Bureau of Economic Geology, Texas University; the apical part of a carina from Wautubbee, Miss., in the Palaeontological Research Institution, Ithaca, N.Y.,; and in the Geological Department of the British Museum (Natural History), fifteen valves:

In. 32536.	Carina.	Wautubbee formation.	Newton, Newton Co., Mississippi.	Presented by A. Wrigley, July 1935.
In. 32537.	Scutum (part of).	,,	,,	,,
In. 37780.	Scutum.	Weches formation.	E. of Robbins road-crossing, Leon Co., Texas.	Presented by Bureau of Economic Geol., Texas Univ., March 1939.
In. 37781.	Rostrum.	Lisbon formation.	Claiborne bluff at old landing, nr. Claiborne, Alabama.	,,
In. 37769–72.	4 carinae,	Weches formation.	Bluff on right bank of Colorado River, nr. Smithville, Bastrop Co., Texas.	,,
In. 37773–74.	2 scuta,			
In. 37775–76.	2 terga,			
In. 37777–79.	3 peduncle plates.			

MEASUREMENTS. Carina (Pl. 13, fig. 1), length 20·4 mm., breadth 4·3 mm.; other incomplete carinae show a probable length of 35 mm. Scutum (Pl. 13, fig. 2), length 21·6 mm., breadth 11·2 mm.; another scutum had a probable length of 25 mm. Tergum (Pl. 13, fig. 3), length, incomplete 14·7 mm., when complete about 16 mm., breadth 7·2 mm.; tergum (Pl. 13, fig. 8), length 14 mm., breadth 7·3 mm. Upper latus (Pl. 13, fig. 9), length 3·1 mm. Rostrum (Pl. 13, fig. 10), length 7·4 mm., breadth 5·8 mm.

DESCRIPTION. Carina (Pl. 13, figs. 1, 4) narrow, length about four and a half times the breadth, with the umbo a little removed from the apex; moderately bowed inwards; basal margin broadly rounded. Tectum moderately convex conversely, bounded on each side by a strong but narrow rounded ridge, and sometimes there is a slight median ridge and other longitudinal ridges. Parietes usually very wide, wider than half the tectum, and in some valves (Pl. 13, fig. 4) the parietes are wider than the tectum; they extend down to the basal angles. In small valves the inner surface is moderately or deeply concave up to the apex, but older valves are very thick and solid and the inner surface is rather shallow.

Scutum (Pl. 13, figs. 2, 5, 7) subtriangular, with the umbo removed about one-seventh the length of the valve from the apex; length under twice the breadth, and a narrow flat ridge extends along the occludent border. A more or less sharp ridge extends from a little below the apex to the tergo-lateral angle, above which the valve is obliquely inclined inwards, and the growth-lines upturned. In some valves two obscure ridges extend from the umbo—one to the inner angle of the basal margin, and the other to about the middle of the lateral margin. Occludent margin weakly convex; basal margin short, forming about a right angle with the occludent margin; tergal margin gently concave, about the length of the lateral margin, which is strongly convex. Outer surface with obscure longitudinal ridges. Inner surface with inner occludent edge rather wide and a little concave.

Tergum (Pl. 13, figs. 3, 8) rather flat, much bowed away from the scutal side, with no definite apico-basal furrow, but the apices of the angles of growth form a curved line, placed about one-third the width of the valve from the carinal margin; a narrow, but rather strong ridge extends from the apex to a point on the scutal margin about two-thirds the distance from the scutal angle; length a little more than twice the breadth. Occludent margin convex, about two-thirds the length of the scutal margin; scutal margin somewhat convex; scutal angle sharp; carinal margin strongly concave, but a little convex towards the sharply rounded basal angle. On the inner surface the inner occludent edge is narrowly raised, steeply inclined, and marked with growth-ridges, and a small part near the apex on the carinal side is similarly, but a little more widely, marked, and these meet in a narrow rounded angle a little below the apex.

Upper latus (Pl. 13, fig. 9) sub-rhomboidal, slightly bowed towards the scutal side, higher than wide, scutal margin concave, and tergal margin slightly convex, both margins bordered by a rounded ridge; basal margin with the two sides forming an acute angle with the apex rounded off. Middle part of valve somewhat raised in a line from the apex to the basal angle. Inner scutal and tergal edges flat and they stand at right angles to the upper surface.

Rostrum (Pl. 13, figs. 6, 10) usually higher than wide, thick and solid, triangular, strongly convex transversely, much bowed inwards, with a strong rounded apico-basal ridge; basal margin strongly excavated in the middle. The sides of the valve are directed upwards and inwards from a raised ridge, and meet one-third the length of the valve from the apex, so that the upper part of the inner margin stands well below, and inwards from, the umbo. This description is based on specimens from the Lisbon formation, near Claiborne, Alabama, but a rostrum from the Upper Weches formation of Smithville, Bastrop County, Texas, is not nearly so thick and solid, although still produced upwards and inwards at the lateral margins. Another valve (Pl. 13, fig. 6), from Claiborne, has the sides produced so much that they lie almost in line with the umbo.

Peduncle (Pl. 13, figs. 13, 14) cylindrical. Pieces of two large peduncles are known; one (Pl. 13, fig. 13) has a length of 27·3 mm. and a breadth (near the upper end) of 9·7 mm., and the other (Pl. 13, fig. 14) a length of 15·6 mm. and a breadth of 7·0 mm. The former seems to be complete so far as the breadth is concerned, and the latter shows the mud infilling of the central part of the peduncle. The more complete peduncle shows that the plates are close-set and arranged more or less in oblique rows, each row slightly curved, with six to seven plates to a breadth of 5·0 mm., and that the outer part of each plate is long and narrow, and finger-like. In side-view (Pl. 13, figs. 11–13) the outer finger-like part of the plate is seen to extend from a laterally flattened block of calcite, somewhat oblong in shape, but tapering towards the inner extremity; the upper part of the oblong block forms a sharp ridge, and from this ridge the block slopes outwards towards another ridge situated about one-third the height of the plate from the top, and each side of the lower part of the plate slopes inwards to form a sharply rounded base. The inner extremity of each plate is irregular in shape, and the plates fit close together; this can be seen on the mud infilling (Pl. 13, fig. 14) where the plates have been broken away leaving a small part still attached to the mud infilling.

REMARKS. Several of the isolated peduncle plates (Pl. 13, figs. 11, 12) were originally sent to me as doubtful Foraminifera, and although they seemed very peculiar, I could not get away from the idea that they were peduncle plates, and they were returned as such with a query. Proof that they were peduncle plates was furnished by the large peduncle of *E. crassissimum* (Pl. 14), for when this was sent to me to find out the group it belonged to, it was clear that it represented a Cirripede peduncle, and that the plates (Pl. 13, figs. 11, 12) although differing in detail were of the same general type as in *E. eocenense.* Subsequently I received the two parts of the peduncle of *E. eocenense* (Pl. 13, figs. 13, 14), and these again furnished the necessary proof. It was not until later that their relationship to the Recent *Euscalpellum rostratum* was recognized.

4. **Euscalpellum crassissimum** n.sp.

PLATE 14, FIGS. 1–5

DIAGNOSIS. An *Euscalpellum* with the peduncle long and comparatively wide, strongly curved, heavily and closely plated for its whole length; inner oblong part of each thick and massive, the outer face as wide as or wider than long. Capitular valves unknown.

DISTRIBUTION. ? Upper Eocene (fossiliferous concretion, with glauconite, occurring in dark shales): east of Boqueron, on south shore of Bahia Inutil, Tierra del Fuego, S. America.

Fossils found with this Cirripede are *Aturia* sp., *Flabellum* cf. *costellatus* (Philipps), and *Teredo*-borings in fossil detrital wood fragments. In a related locality a specimen of *Turnus* (*Xylophagella*) was found, said to bear a striking resemblance to a species in the Upper Cretaceous of N. America.

HOLOTYPE AND MATERIAL. A large peduncle (No. 3412) in the Palaeontological Research Institution, Ithaca, New York, sent to me for study by Dr. Katherine Van Winkel Palmer, through the kind permission of the Standard Oil Co. of New Jersey.

MEASUREMENTS. Peduncle: length, 104·0 mm.; breadth, 30·0 mm., and where broken obliquely across near the top of the peduncle, 66·0 mm. Individual plate from upper part of peduncle: height of outer face, *circa* 5·0 mm., breadth of same, 4·2 mm., length of inner extension, 7·5 mm., height of same, 3·5 mm.

DESCRIPTION. This is a large and massive peduncle (Pl. 14, figs. 1–5) partially enclosed in a nodule, and shows the whole of one side and part of the other. It is incomplete both at the top and base. The peduncle is comparatively wide, cylindrical, strongly curved, and heavily plated for its whole length. Individual plates thick and massive, obliquely inclined downwards, the inner projecting part formed of an oblong block of calcite, very like an Asteroid ossicle (Pl. 14, figs. 3, 4), although tapering a little towards its inner end; outer face in most plates as wide as or wider than long, but a few plates are attenuated above, although wide at the base, and they somewhat project. With such close-set and massive plates the peduncle is consequently very strong and solid, and at the base (Pl. 14, fig. 5) there is only a narrow median canal.

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PLATE 11

Euscalpellum zelandicum n.sp.

Upper Cretaceous, Teurian (Upper Senonian), Greensand:
Waipara Gorge, North Canterbury, New Zealand.

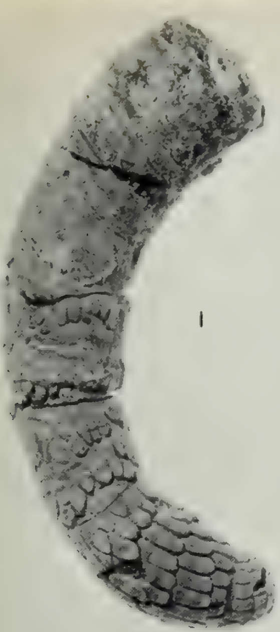
Collected by Dr. C. T. Trechmann

FIG. 1. Peduncle (nearly complete). Holotype. Nat. size. In. 43731.

FIG. 2. Peduncle (complete except probably at extreme base). Nat. size. In. 43732.

FIGS. 3*a–c*. *a*, Peduncle (upper half); *b*, upper end showing deep cavity; *c*, broken basal end of same. Nat. size. In. 43733.

[M. G. Sawyers photo.]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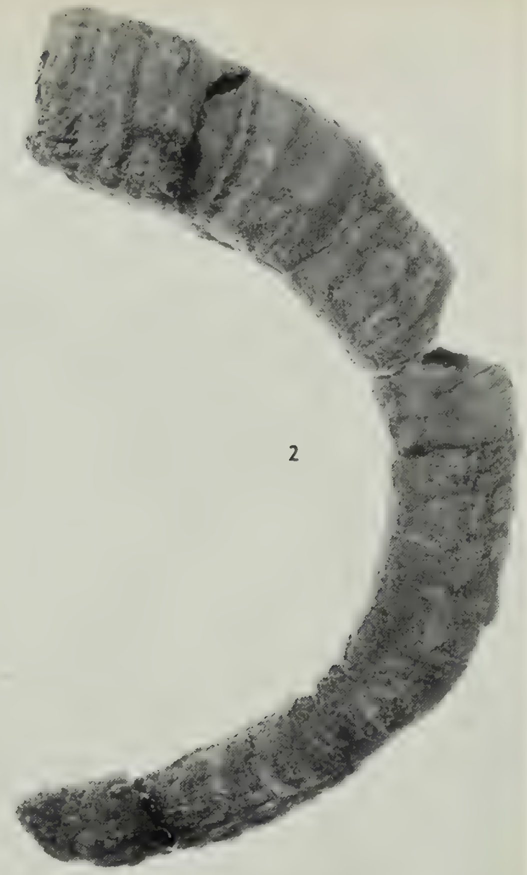
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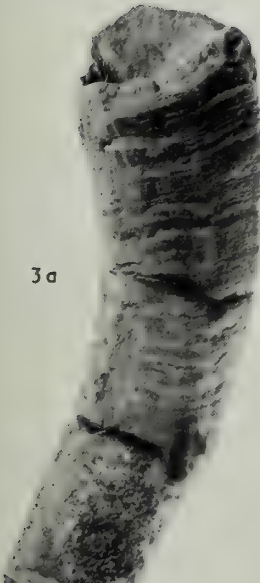
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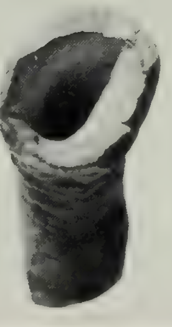
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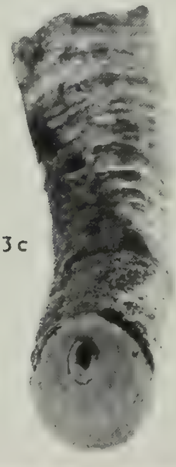
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EUSCALPELLUM ZELANDICUM

PLATE 12

Euscalpellum zelandicum n.sp.

Upper Cretaceous, Teurian (Upper Senonian), Greensand:
Waipara Gorge, North Canterbury, New Zealand.

FIGS. 1*a*, *b*. *a*, Peduncle (basal part to show plates); *b*, probable base. × 1·5 diam. Collected by C. W. Weston. In. 43734.

Euscalpellum antarcticum n.sp.

Upper Cretaceous, Upper Senonian: The Naze, NW. Graham Land, Antarctica.

Collected by W. N. Croft.

FIGS. 2*a*, *b*. Peduncle (part of, longitudinally broken). Holotype. *a*, outer view; *b*, inner view showing shape of plates. Nat. size. D97.4A. In. 43813.

FIG. 3. Peduncle (part of). Outer view. Nat. size. D85.7. In. 43814.

FIGS. 4*a*, *b*. Peduncle (part of). *a*, Outer view; *b*, top view of same. Nat. size. D86.8. In. 43815.

[M. G. Sawyers photo.]

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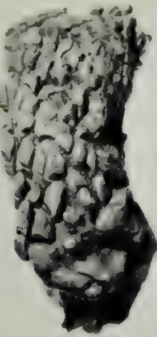

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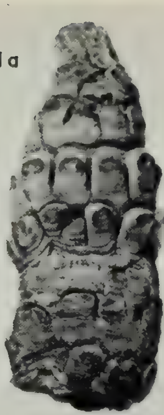

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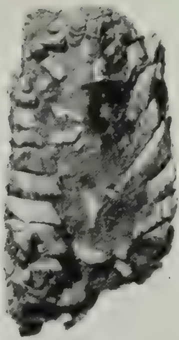

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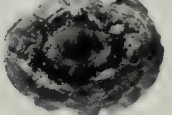

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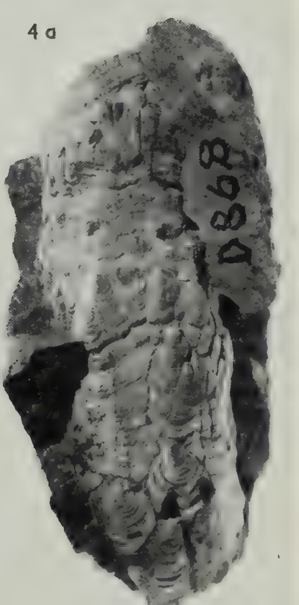

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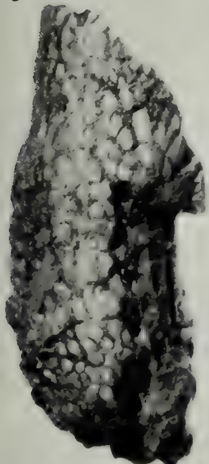

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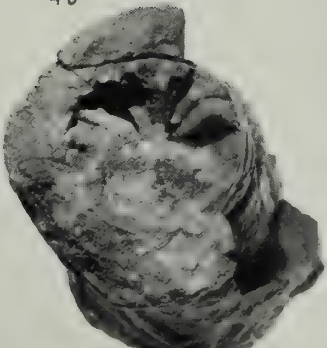

EUSCALPELLUM ZELANDICUM (FIG. 1) AND E. ANTARCTICUM (FIGS. 2–4)

PLATE 13

Euscalpellum eocenense (Meyer)

Middle Eocene, Claiborne group, Wautubbee formation:
Wautubbee, Clarke Co., Mississippi.

FIG. 1. Carina. *a*. outer view; *b*, side view. × 2 diam.

FIG. 2. Scutum (right). Outer view. × 2 diam.

FIG. 3. Tergum (right). Outer view. × 2 diam.

Middle Eocene, Claiborne group: Claiborne, Alabama.

FIG. 4. Carina. Side view. × 2 diam.

FIG. 5. Scutum (left). Outer view. × 2 diam.

FIG. 6. Rostrum. Outer (apical) view. × 2 diam. (Original of Meyer, 1885: 70, figs. *c*, c^1).

Middle Eocene, Claiborne group, Weches formation: 5·2 miles W. of
Centerville, Leon Co., Texas (Loc. 135-T-38).

FIG. 7. Scutum (right). *a*, outer view; *b*, inner view. × 2 diam.

FIG. 8. Tergum (left). *a*, outer view; *b*, inner view. × 2 diam.

Middle Eocene, Claiborne group, Weches formation: Colorado
River bluff, Smithville, Bastrop Co., Texas (Loc. 11-T-2).

FIG. 9. Upper latus (left). Outer view. × 4 diam.

Middle Eocene, Claiborne group, Lisbon formation: Claiborne bluff
at old landing, near Claiborne, Alabama.

FIG. 10. Rostrum. *a*, outer view; *b*, inner view; *c*, side view. × 2 diam.

(The originals of figs. 1–6 are in the Geol. Surv. of Alabama (Meyer colln.), and the originals of figs. 7–10 are in the Bureau of Economic Geology, Texas University.)

Middle Eocene, Claiborne group, Weches formation: Colorado
River bluff, Smithville, Bastrop Co., Texas.

FIGS. 11, 12. Peduncle plates. Side views. × 4 diam.

Middle Eocene, Claiborne group, Wautubbee formation:
Wautubbee, Clarke Co., Mississippi.

FIGS. 13, 14. Peduncle (parts of). *a*, outer view; *b*, inner view. × 2 diam.

(Originals of figs 11–14 are in the Bureau of Economic Geology, Texas University.)

[M. G. Sawyers photo.]

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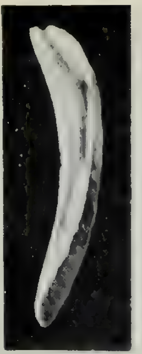
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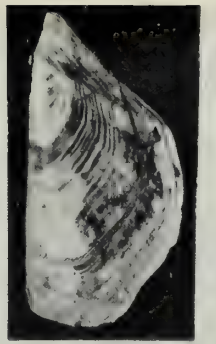
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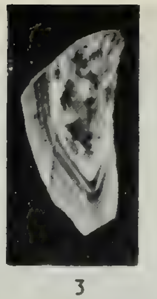
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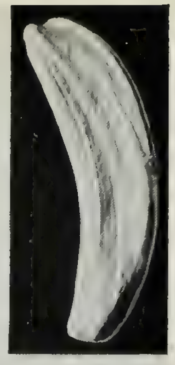
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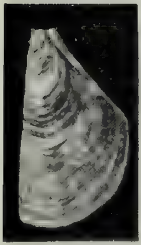
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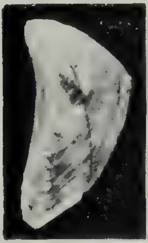
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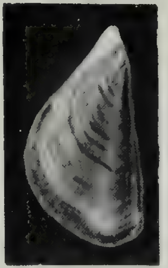
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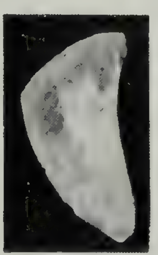
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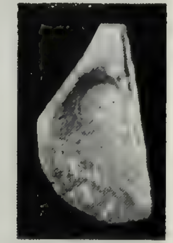
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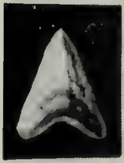
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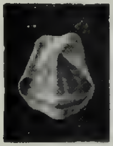
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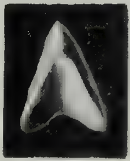
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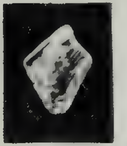
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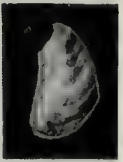
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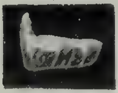

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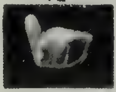

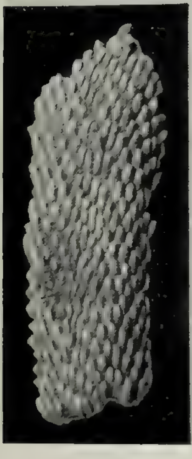
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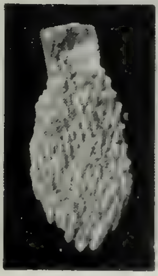

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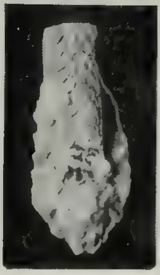

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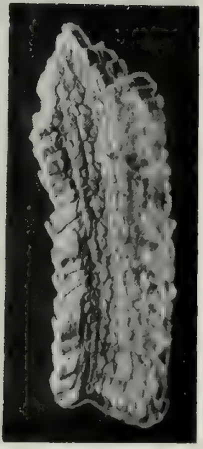


EUSCALPELLUM EOCENENSE

PLATE 14

Euscalpellum crassissimum n.sp.

? Upper Eocene: east of Boqueron, on south shore of Bahia Inutil, Tierra del Fuego, S. America.

Fig. 1. Peduncle. Side view. Nat. size.

Fig. 2. Same. End view. Nat. size.

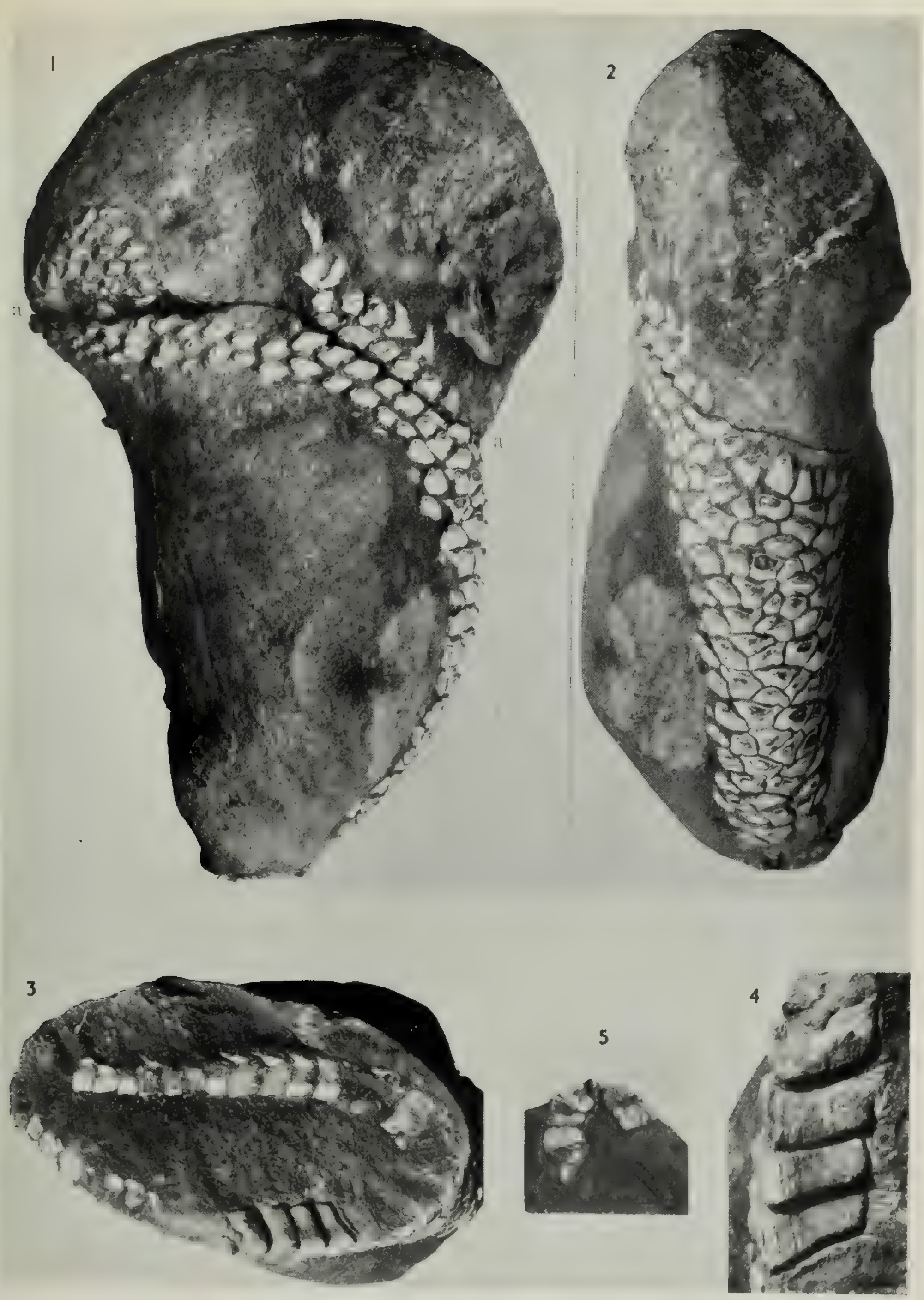
Fig. 3. Same. Top of lower part where broken obliquely across peduncle *a-a*, and showing four complete plates. Nat. size.

Fig. 4. Enlarged view of the four plates. × 2 diam.

Fig. 5. Same. Basal end (broken). Nat. size.

(Original in Palaeontological Research Institution, Ithaca, New York, No. 3412.)

[M. G. Sawyers photo.]



EUSCALPELLUM CRASSISSIMUM

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GREAT BRITAIN
AT THE
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OXFORD
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BRITISH MUSEUM
NATURAL HISTORY

15 AUG 1951

SOME JURASSIC AND CRETACEOUS CRABS (PROSOPONIDAE)

T. H. WITHERS

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GEOLOGY Vol. 1 No. 6
LONDON : 1951

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BY

THOMAS H. WITHERS

Pp. 171–192; *Pls.* 15–17; 14 *Text-figures*

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SOME JURASSIC AND CRETACEOUS CRABS (PROSOPONIDAE)

By THOMAS H. WITHERS

(*With Plates* 15–17)

SYNOPSIS

Further evidence is given of the structure of the early Middle Jurassic Crabs, *Pithonoton richardsoni* and *Prosopon mammillatum*, and the Lower Cretaceous *Mithracites vectensis*; and a new Upper Cretaceous species, *Rathbunopon woodsi*, is described; all belonging to the family Prosoponidae. The additional evidence shown by these Crabs adds much to our knowledge of their structure, as well as to our knowledge of the evolution of the group.

INTRODUCTION

When my paper on the Lower Lias *Eocarcinus praecursor* was written (1932), it was not then possible to compare it adequately with some of the Middle and Upper Jurassic species, for little of those species was known except for the cephalothorax, and what was known often gave a false idea of their structure. Since then I have from time to time paid some attention to several of these forms.

Development, by means of a needle, of the next earliest British Crab, *Pithonoton richardsoni*, added further details of its structure, and the discovery of a second specimen confirmed these findings, for the orbital regions and the hepatic lobe are well preserved.

Development of the holotype and other specimens of *Prosopon mammillatum*, and the discovery in the British Museum collections of a cephalothorax showing the complete left side and of an abdomen, adds considerably to our knowledge of that Crab.

The most striking success was with the Lower Cretaceous (Aptian) *Mithracites vectensis*, for the development of a number of specimens led to the disinterment of the limbs and appendages of this Crab, including one of the last (reduced) pair of legs, and even the maxillae, so that a complete reconstruction could be given (Text-fig. 14).

All this new information adds a great deal to our knowledge of these early Crabs of the family Prosoponidae, as well as to our knowledge of the evolution of the group.

I am indebted to Dr. M. F. Glaessner for kindly reading through some of the manuscript; to Mr. A. G. Brighton and Mr. Henry Woods; to Professor W. F. Whittard; to Mr. D. T. Donovan, who, when he learned that I was working on *Pithonoton richardsoni*, most generously arranged for the second specimen, which he was about to describe, to be sent to me for description; and to Professor H. B. Stenzel for assistance with *Rathbunopon woodsi*.

Tribe BRACHYURA Latreille

Sub-tribe DROMIACEA De Haan

Super-family DROMIIDEA Alcock

Family Prosoponidae von Meyer

Genus *PITHONOTON* von Meyer

Genotype. *P. marginatum* von Meyer, 1842: 71. Upper Jurassic (Tithonian): Württemberg.

Diagnosis. Cephalothorax convex transversely and longitudinally. Cervical and branchio-cardiac furrows equally strong. Front broad and straight in typical species. Posterior margin comparatively narrow. Lateral margin weakly developed, never reaching the branchio-cardiac furrow. Sulci for eyes usually well developed.

Pithonoton richardsoni (H. Woodward)

(Plate 15, figs. 1–6; Text-figs. 1–3)

1907 *Prosopon richardsoni* H. Woodward, p. 80, figs. 1, 2.
1907 *Prosopon richardsoni* H. Woodward: Richardson, p. 82.
1925 *Pithonoton richardsoni* (H. Woodward) Van Straelen, p. 361.
1929 *Pithonoton? richardsoni* (H. Woodward): Glaessner, p. 324.
1933 *Pithonoton? richardsoni* (H. Woodward): Glaessner, p. 181.

Diagnosis. A *Pithonoton* with elongated cephalothorax; orbito-frontal part produced into a wide angle for the rostrum is extended in front to a point; rostrum not downturned as in the genotype *P. marginatum* (Text-figs. 4–6), and in *P. grande* (Text-figs. 7–9), and leaving the front bilobed.

Distribution. Middle Jurassic, Bajocian, Inferior Oolite, not found *in situ*, but probably from the Doulting Beds, *Anabacia*-Limestone '*Clypeus*-Grit': Tor Hill, near Wotton-under-Edge, south Cotswolds. Inferior Oolite, *truelli* sub-zone, Upper Coral Bed: 200 yards E. of Walnut Farm, Dundry Hill, Somerset; this is very near the presumed horizon of the holotype.

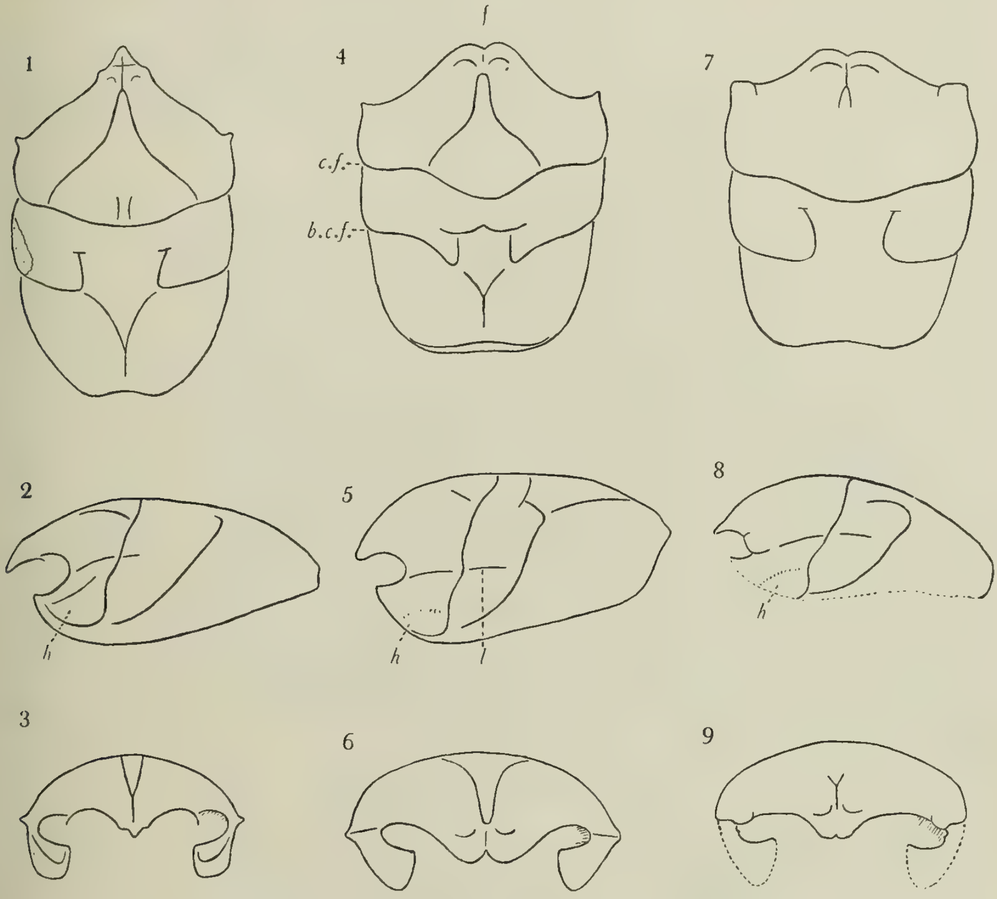
Holotype. The cephalothorax figured by H. Woodward in the Geological Department of the British Museum (collected by C. L. Walton and presented by L. Richardson), In. 17026.

Material. The holotype, and a cephalothorax in Bristol University (Geol. Dept.), collected by T. R. Fry.

Measurements. Cephalothorax (holotype), length 20 mm., breadth 13 mm. Cephalothorax (Bristol Univ.), length 15·8 mm. (incomplete), breadth 12·4 mm.

Remarks. This is the earliest of the British Oolitic Crabs. H. Woodward first described the species under the genus *Prosopon*, but Van Straelen referred it to the genus *Pithonoton*. There has been some doubt about the generic reference, mainly because of the lack of knowledge of certain characters, and this probably led Glaessner to refer the species to *Pithonoton* with a query. In my opinion, based on the new evidence, it is a primitive form of *Pithonoton*. H. Woodward's figure of the cephalothorax is incorrect in its proportions, especially of the mesogastric lobe, and the several regions were wrongly named by him.

Description. The holotype (Pl. 15, figs. 1–3; Text-fig. 1) is a decorticated cephalothorax, with the shell preserved only at the tip of the rostrum and on the left margin of the branchio-cardiac region. This specimen was developed by me to some extent to show the fronto-orbital margin, and it was apparent that the orbits must have been shallow (Pl. 15, fig. 2) for the orbital surface is flat; further cleaning showed the cervical furrow beginning to curve upwards (Pl. 15, fig. 3) to enclose the hepatic lobe, which was badly preserved, and the lateral margin was only barely indicated.



Text-figs. 1–3. *Pithonoton richardsoni* (H. Woodward).

Fig. 1, outer view, Holotype, Brit. Mus., In. 17026; Fig. 2, side view; Fig. 3, fronto-orbital view; Figs. 2, 3, based on specimen in Bristol University.

Text-figs. 4–6. *Pithonoton marginatum* von Meyer.

Fig. 4, outer view; Fig. 5, side view; Fig. 6, fronto-orbital view. Based on specimen, Brit. Mus., In. 38253. Upper Jurassic, Tithonian: Stramberg, Moravia.

Text-figs. 7–9. *Pithonoton grande* von Meyer.

Fig. 7, outer view; Fig. 8, side view; Fig. 9, fronto-orbital view. Based on specimen, Brit. Mus., In. 36846. Upper Jurassic, Tithonian: Stramberg, Moravia.

(*cf.*, cervical furrow; *bcf.*, branchio-cardiac furrow; *f.*, front; *h.*, hepatic lobe; *l.*, lateral margin).

Figs. 1–3, ×2·5 diam.; Figs. 4–6, ×3·0 diam.; Figs. 7–9, ×0·5 diam.

At this stage Mr. D. T. Donovan kindly caused the second-known specimen to be sent to me. This is also a decorticated cephalothorax (Pl. 15, figs. 4–6; Text-figs. 2, 3), rather worn, and perhaps a little flattened dorsally, judging by the holotype, but the shell is preserved in the orbital regions and along the left side below the lateral margin; the surface is very finely granulated and pitted. Sides of cephalothorax steep and incline inwards. The orbits are comparatively shallow and the lower orbital margin extends anteriorly well beyond the upper orbital margin; there is a slight fissure on the orbital margin, and the outer orbital spine is broken off. Hepatic lobe well developed, situated below the lateral margin, and the cervical furrow curves under it (Pl. 15, fig. 6; Text-fig. 2).

Cephalothorax elongated, a little under one and a half times as long as wide. Front produced into a wide angle, for the rostrum is extended in front, and not sharply downturned; the lateral edges of the rostrum are prominent, for from these edges the surface slopes steeply towards the median longitudinal rostral furrow; on each side of the rostrum near the base there is produced a long, low node. Fronto-orbital margin concave above, and convex below, ending at the prominent outer orbital spine. Antero-lateral margin short and convex. Cervical and branchio-cardiac furrows equally strong, the latter curving downwards nearly to the posterior margin. Mesobranchial lobe wide, more than twice the width of the gastric region on each side, and well defined by a furrow on each side; there is a slight indication of a short median longitudinal depression at the base. Urogastric furrows short, and not deeply defined. Posterior margin rather broken, but probably about half the greatest width of the cephalothorax. Orbits comparatively shallow, divided off on the inner side by the frontal margin which curves downwards, reminding one of this feature which is so well shown in specimens of *Dromiopsis* (Dynomenidae); lower orbital margin extending well beyond the upper orbital margin. Lateral margin weakly developed anteriorly, and dying out less than half-way to the branchio-cardiac furrow. There seems to be no justification for the four tubercles on the 'cardiac' region seen in Woodward's figure.

Genus ***PROSOPON*** von Meyer

Genotype *P. tuberosum* von Meyer, 1840: 21. Lower Cretaceous, Neocomian: Boucherans (Jura), France.

Diagnosis. Cephalothorax strongly vaulted. Branchio-cardiac furrow more strongly developed than cervical furrow. Front narrow. Posterior margin broad. Lateral margin not developed. Sulci for eyes absent.

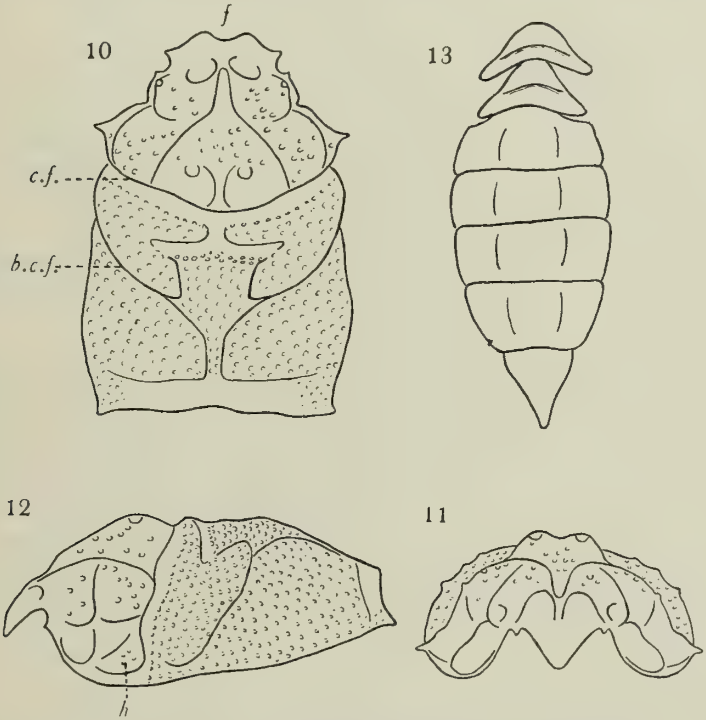
Prosopon mammillatum H. Woodward

(Plate 16, figs. 1–4; Text-figs. 10–13)

1868 *Prosopon mammillatum* H. Woodward, p. 3, pl. 1, figs. 2, 2*a*.
1877 *Prosopon mammillatum* H. Woodward: H. Woodward, p. 6.
1925 *Avihomola mammillata* (H. Woodward) Van Straelen, p. 340.
1929 *Protocarcinus mammillatus* (H. Woodward) Glaessner, p. 349.
1933 *Prosopon mammillatum* H. Woodward: Glaessner, p. 180.

Diagnosis. A *Prosopon* with the lobes of the cephalothorax strongly protuberant, a prominent spine on each hepatic lobe, and two large spines towards the base of the mesogastric lobe; surface coarsely granulated.

Remarks. *Prosopon mammillatum* was described as long ago as 1868, and since that date nothing further has been added to our knowledge of it. Van Straelen (1925: 340) referred the species to his genus *Avihomola*, which is a synonym of Woodward's genus *Protocarcinus* (1865). Glaessner (1929: 349) referred the species to *Protocarcinus*, and later (1933: 180) to the genus *Prosopon*. It has not been possible for me to see the genotype of *Prosopon* (*P. tuberosum*).



Text-figs. 10–13. *Prosopon mammillatum* H. Woodward.

Fig. 10, outer view; Fig. 11, fronto-orbital view; Fig. 12, side view; Fig. 13, abdomen. (*c.f.*, cervical furrow; *b.c.f.*, branchio-cardiac furrow; *f.*, front; *h.*, hepatic lobe.) Figs. 10–12 × 1·5 diam.; Fig. 13, nat. size.

Distribution. Middle Jurassic, Middle Bathonian, Great Oolite, Stonesfield Slate: Stonesfield, Oxfordshire.

Holotype. A cephalothorax in the Sedgwick Museum, Cambridge, B. 2719.

Material. In the British Museum are two examples of the cephalothorax (44291, Morris colln.; 59664, Hon. R. Marsham colln.); the left half of a cephalothorax, In. 28821; the left branchial part of the largest-known cephalothorax (I. 269, Sir P. de M. G. Egerton colln.); three fragments of the cephalothorax (59664, I. 3289, In. 28822), and a complete female abdomen (I. 3048, P. B. Brodie, *ex* Stutchbury colln.)

MEASUREMENTS. Holotype, length, including the rostrum, 34 mm.; breadth 24 mm. Specimen In. 28821, Pl 16, fig. 2, length, including rostrum, but slightly incomplete posteriorly, 44 mm. Specimen I. 269 measures 31·5 mm. from the cervical furrow to the posterior margin, so the complete cephalothorax would measure about 55 mm. Abdomen, length 52·5 mm.

DESCRIPTION. The holotype of *Prosopon mammillatum* is a cephalothorax showing the dorsal surface and retaining its original convexity. Woodward's figure shows two spines on each side, one apparently projecting from the protogastric lobe, and the other from the frontal part of the cephalothorax. Actually, those on the left side were not seen in the specimen, but the right posterior spine is preserved and is produced from the hepatic lobe. Careful development of the anterior part of the holotype has exposed two comparatively large epigastric lobes, followed by a wide, tongue-shaped, and strongly downturned rostrum. Woodward's figure showing a two-spined rostrum is therefore wholly inaccurate. At the base of the rostrum, on the left side, a wide, flattened, triangular spine has now been exposed, but that on the right side is broken off, and below its level lies what may or may not be the basal part of an eye-stalk. It was on this latter that Woodward may have based his anterior spines.

Two examples of the cephalothorax in the British Museum (Nos. 44291, 59664) show only the dorsal surface, and although they are a little more flattened than the holotype, they exceed it in size. More important is a cephalothorax (In. 28821) much larger than those above, preserved as a cast and showing little more than the left side, except that the rostrum is entire, and nearly all of the mesogastric lobe is preserved. Its importance lies in the fact that it is the only known specimen which shows the whole of the antero-lateral and branchial margins, and this not only allows us to see how cylindrical the cephalothorax really is, but more important still, the direction of the cervical and branchio-cardiac furrows, and the hepatic lobe.

In addition there is a female abdomen which has been cleaned to show all the segments; it is not attached to any cephalothorax, but since *Prosopon mammillatum* is the only crab known to occur in the Stonesfield Slate, and is known by the remains of at least eight examples of the cephalothorax, and considering their correspondence in size to this abdomen, there can be little doubt that it belongs to the same species. The abdomen has a length of 52·5 mm., and must have belonged to an individual exceeding in length the largest known cephalothorax. *Prosopon mammillatum* is therefore the largest of the known Upper Jurassic Crabs, even larger than the Lower Liassic *Eocarcinus*, and as will be shown later, throws further light on the phylogeny of the Brachyura.

Cephalothorax cylindrical, with steep sides; almost one and a half times as long as wide, widest at its posterior third, convergent in front; very strongly convex transversely; moderately convex longitudinally. Rostrum comparatively wide, tongue-shaped, somewhat excavated, strongly downturned in front, with a prominent, flattened, and triangular spine on each side at the base, just in front of the epigastric lobes. These wide basal spines evidently served for the protection of the eye-stalk. No sulci for eyes. Regions and furrows distinctly marked, the regional lobes very prominently raised. Cervical furrow strongly marked, continuous, wide and deep, obtusely V-shaped. Branchio-cardiac furrow well defined, but not so wide and deep as the cervical, and near the antero-lateral margin is directed slightly backwards and abruptly forwards to meet the cervical furrow; above this junction is the large hepatic lobe. Surface ornamented with fairly coarse granules. Two comparatively large epigastric lobes are seen behind the base of the rostrum. On the swollen mesogastric lobe, two large prominences, evidently the bases of broken-off spines, are situated at the wide posterior end, and a small prominence is situated near the base of the narrow triangular process; the remainder of the lobe has several irregularly placed tubercles. Hepatic lobe swollen and prominent and divided transversely and obliquely by a ridge into two almost equal parts, the outer part having a prominent spine on its outer margin, well seen in dorsal view. Above the hepatic lobe is a smaller lobe bounded above by the orbital margin. Protogastric lobe rounded and prominent, bounded posteriorly by the cervical furrow. Urogastric lobe with two comparatively small tubercles separated by a deep, wide depression, and the cardiac lobe is rather swollen, with deep lateral furrows, and bears two small tubercles near the base. Antero-branchial lobe with a deep depression close to the urogastric lobe, and bounded laterally by the cardiac furrow.

Abdomen comparatively broad (length 52·5 mm.; greatest breadth, at the fourth segment, 22·5 mm.), with seven separate segments. The first two segments are comparatively long and narrow, divided transversely by a groove across the middle, strongly excavated at the sides, so that the basal angles are acute and free; the third to sixth segments increase in height, the sixth being the longest, and their lateral margins form a continuous curved line, or in other words the lateral margins are not free; the seventh segment is acutely triangular. There is some convexity of the surface down the middle of the third to sixth segments. The excavation of the first two segments shows that the abdomen was not entirely folded under the cephalothorax, and indicates that the last pair of legs were reduced and carried elevated on the back.

Genus ***RATHBUNOPON*** Stenzel

Genotype *R. polyakron* Stenzel, 1945: 450. Lower Cenomanian, Comanche Series, Washita Group, Grayson Marl: northwestern Austin, Travis Co., Texas.

Diagnosis (after Stenzel). Carapace ovoid in outline, slightly longer than wide; fronto-orbital width about three-quarters of width. Frontal rostrum short, barely projecting, triangular, and with a median groove. Orbits well defined, about twice as wide as high, with two notches on the upper margin and a projecting dentiform tubercle on the lower margin. Lateral margins of carapace poorly defined. Cervical and other grooves deep. Urogastric and metagastric regions well separated and of the shape of transverse bars. Mesobranchial region bilobed toward the cardian grooves. Metabranchial regions large, confluent or nearly confluent at midline.

Rathbunopon woodsi n. sp.

(Plate 16, figs. 5, 6)

Diagnosis. A *Rathbunopon* like *R. polyakron* but with the cephalothorax more strongly convex transversely, orbito-frontal part more constricted; rostrum narrower, slightly longer, with straighter sides; cardiac lobe longer, with posterior end more sharply pointed, and with postero-lateral delineation of the lobe less convexly curved; orbital margin with two well-defined tubercles.

DISTRIBUTION. Cenomanian, upper *varians* zone (Meyer's Bed 12): Beer Head, Devonshire.

HOLOTYPE. A decorticated cephalothorax in the Sedgwick Museum, Cambridge (Meyer colln.), B. 50,779.

MEASUREMENTS. Length, including rostrum, 18·8 mm.; breadth, 15·3 mm.; fronto-orbital breadth, 9·0 mm.

DESCRIPTION. Cephalothorax sub-ovate, a little longer than wide, much convergent anteriorly, widest at its posterior third, strongly convex transversely and moderately convex longitudinally. Front produced into a comparatively narrow tongue-shaped rostrum, which is strongly downturned, its edges prominently raised; rostrum with a slight median longitudinal furrow, and near the middle of each side is produced into a long, low tubercle. Outer orbital spine prominent. Orbital margin less than the width of the base of the rostrum, with two well-defined tubercles, close together, and divided by a fissure. Orbits large and deep. Antero-lateral margins strongly convergent, with a large tubercle on the outer margin of the mesobranchial lobe taking up almost the whole of the space between the cervical and branchio-cardiac furrows; postero-lateral margins protuberant; posterior margin moderately convex, much wider than the fronto-orbital margin, with a narrow, raised marginal rim, bounded above by a very wide depression. No definite lateral margin developed.

Since the surface of the shell is only preserved in places, the specimen is almost in the form of an internal cast, but the surface must either have been smooth or only very finely granulated. Regions and furrows distinctly marked. Branchio-cardiac furrow very deep. Cervical furrow well developed above the mesobranchial region; it then extends round the top of, and to below, the large outer mesobranchial tubercle, and is then directed forwards at the branchio-cardiac furrow to enclose the low hepatic lobe (seen only in side view) in front of it. A small but prominent tubercle is situated on each epigastric lobe, and each tubercle is separated by a wide space from two close tubercles on the upper orbital margin; the two latter are separated by a deep fissure. A large tubercle is placed on each protogastric lobe; a triangle of three tubercles on the mesogastric lobe, which is fairly well defined by lateral furrows. Mesobranchial lobe bilobed towards the gastric region, the upper limb forming a large boss, and the lower limb slender; near the outer end of the lower limb there is a somewhat transverse depression. A large outwardly directed tubercle is situated on the outer margin of the mesobranchial lobe. Metagastric bar a little longer than the urogastric bar, and confluent with the mesobranchial boss. Urogastric bar separated from the metagastric bar by a fairly deep furrow, and by a deeper furrow from the cardiac lobe. Metabranchial region devoid of tubercles. Cardiac lobe is in the form of an inverted and somewhat acute triangle, with no trace of pits, and bounded by deep lateral furrows. Intestinal lobe small, somewhat triangular, and situated almost wholly in the wide depression above the posterior margin.

In the Geological Department of the British Museum there is a specimen (No. 24657) represented by a worn internal cast (Pl. 16, fig. 7) from the Albian (Gault) of Folkestone, Kent. It closely agrees with the above species, but it appears to differ in that the metagastric bar is not apparent, and the cardiac lobe is slightly larger. Nothing more can be done with such an ill-preserved specimen.

Comparison with other species. This species is very close to the genotype *Rathbunopon polyakron*, but since the holotype of that species is a cephalothorax with well-preserved surface, and the present species, *R. woodsi*, is founded on a decorticated, but uncrushed specimen, the differences may be partly, but not wholly, illusory. *R. woodsi* has the cephalothorax more strongly convex transversely, and the fronto-orbital part more constricted; rostrum narrower, slightly longer, with straighter sides; cardiac lobe longer, with posterior end more sharply pointed, the postero-lateral delineation of the lobe less convexly curved, and no trace of pits; orbital margin with two well-defined tubercles, but *R. polyakron* has these same tubercles feebly indicated; metagastric bar confluent with the mesobranchial boss, but in *R. polyakron* the ends of the metagastric bar are pinched off from the mesobranchial boss, and the groove separating the urogastric bar from the mesobranchial region is deeper; branchio-cardiac furrow with more definite upward sweep; mesobranchial lobe bilobed, but with the lower limb longer and more slender; intestinal lobe placed in a more posterior position; metagastric lobe slightly longer than the urogastric lobe; large tubercle on outer margin of mesobranchial region more prominent and more widely spaced from the protogastric tubercle.

Genus ***MITHRACITES*** Gould

Diagnosis. A Prosoponid with the cephalothorax sub-circular, moderately convex transversely and longitudinally, posterior margin wide and convex. Lateral margin distinctly developed. Front produced into a wide tongue-shaped rostrum, slightly downturned. Sulci for eyes wide, somewhat rounded and shallow, the sub-orbital margin produced well beyond the supra-orbital margin. Last pair of pereiopods reduced and elevated on the back.

Remarks. This monotypic genus was first described by Gould (1859) and based on the species *M. vectensis* Gould, represented only by a poorly preserved cephalothorax. Two similar specimens were figured by Bell (1863), and Carter (1898) added to Bell's description. Woodward (1874) mentions more complete specimens which were not subsequently described.

The systematic position of this Crab has been rather doubtful, and this is no doubt due to the poor preservation of the specimens so far figured. Some twenty-two specimens in the Geological Department of the British Museum have been prepared by me—some of these were probably those mentioned by Woodward—and from these specimens it is now possible to make known its structure, and to give a reconstruction of the entire crab.

Mithracites vectensis Gould

(Plate 17, figs. 1–5; Text-fig. 14)

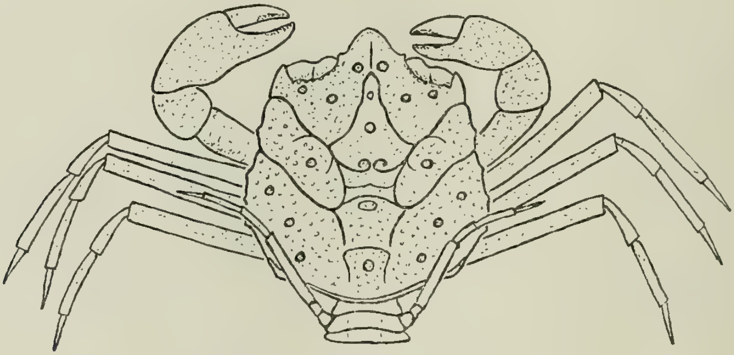
1859 *Mithracites vectensis* Gould, p. 237, figs. 1–3.
1863 *Mithracites vectensis* Gould: Bell, p. 1, figs. 2, 3.
1874 *Mithracites vectensis* Gould: H. Woodward, p. 307.

1877 *Mithracites vectensis* Gould: H. Woodward, p. 14.
1898 *Mithracites vectensis* Gould: Carter, p. 32.
1929 *Mithracites vectensis* Gould: Glaessner, p. 259.

DIAGNOSIS. Same as for the genus.

DISTRIBUTION. Lower Cretaceous (Aptian), *deshayesi* zone, Lower Greensand: Atherfield, Isle of Wight.

GENOHOLOTYPE. A cephalothorax in the Geol. Dept. of the British Museum (presented by J. Middleton), In. 28837. The original of Bell's fig. 2 (59771) and fig. 3 (In. 28841) are in the same collection.



TEXT-FIG. 14. *Mithracites vectensis* Gould.
Reconstruction, based on specimens figured Pl. 17, figs. 1–5. ×1·5 diam.

MATERIAL. In addition to the above three specimens, there are nineteen specimens in the same collection in varying states of preservation.

DESCRIPTION. Cephalothorax sub-circular, and when uncrushed and including the rostrum, very little longer than wide, widest at its posterior third; moderately convex transversely, and a little more strongly longitudinally. Front produced into a comparatively wide tongue-shaped rostrum, which is a little downturned; the edge is raised and prominent, especially anteriorly, and there is a median longitudinal depression, and a small low spine on each side at the base of the rostrum. Orbital margin concave, wider than the base of the rostrum, and partly defined by a ridge of small tubercles extending from the base of the rostrum and ending at a wide shallow notch near the outer orbital spine. Outer orbital spine prominent. From the supra-orbital margin the sulci for the eyes extend downwards and outwards well beyond the supra-orbital margin; the sulci for the eyes are therefore wide and shallow, somewhat rounded, divided by an oblique furrow into two halves and ending in a notch at the sub-orbital margin (Pl. 17, fig. 1 *b*). Antero-lateral margins very slightly convergent, with a single small tubercle near the branchio-cardiac furrow; postero-lateral margins strongly convex, protuberant, with a row of three tubercles on the anterior two-thirds; posterior margin slightly convex, comparatively wide, with a narrow raised marginal rim. Lateral margins well developed.

Regions and furrows distinctly marked. Surface ornamented with fine irregularly spaced tubercles, which on the larger prominences are closely set. Of the large tubercles, one is situated on each epigastric lobe immediately behind the base of the rostrum, and two on each protogastric lobe; a single small tubercle is placed on the triangular process of the mesogastric lobe, followed behind by a large tubercle; two tubercles, separated by a longitudinal depression, are placed at the base of the mesogastric lobe; a large tubercle is placed on the cardiac lobe, and the intestinal lobe forms a large rounded prominence separated from the cardiac lobe by a deep and curved furrow; a single tubercle is situated on each antero-branchial lobe, nearer to the cardiac furrow, and a curved longitudinal line of three tubercles is seen on the postero-branchial lobe.

Abdomen not entirely folded under the cephalothorax, broad in both sexes, the segments distinct; female with the seventh segment (telson) almost flat and obtusely triangular, nearly twice as wide as long, but in the male this segment is deeply excavated towards its base and is almost as long as wide. There are no intercalated plates (uropods) between the sixth segment and the telson such as are seen in the family Dromiidae.

Ischium of third maxillipede with a deep oblique longitudinal groove extending from the middle of the anterior margin to near the base of the outer margin; exopodite slender, with a median longitudinal carina. Details of antennary regions and buccal-frame are seen in the specimen figured Pl. 17, figs. 3 *b*, *c*; the buccal-frame and mandibles are seen in the specimen figured Pl. 17, fig. 4.

Chelipeds (1st pereiopods) slightly unequal, the left a little larger than the right in specimen In. 28832 (Pl. 17, fig. 3), finely granulated, merus short and stout; carpus short and rounded; propodus strongly convex outwardly, with the palm flattened. Fingers little more than half the length of the hand, with a single large, low tooth.

Pereiopods (2nd–4th) flattened laterally, with the dactylus slender and pointed; 5th and last pereiopod much reduced, about one-third the length of the others, and carried elevated on the back.

PHYLOGENY

The Lower Lias *Eocarcinus praecursor* is by far the geologically oldest crab and is more complete than any other Jurassic crab. Although crabs have been found in the succeeding Bajocian, Bathonian, and Tithonian rocks, they are, except for the Upper Bathonian *Prosopon auduini* (Eudes-Deslongchamps), known only by their cephalothorax. In most species the cephalothorax shows only the dorsal surface, and since in some the fronto-orbital part is incompletely exposed, the published figures often give a false idea of their real structure. Many of the Jurassic species require study and redescription.

The next earliest form is *Pithonoton*, and crabs of this genus have a simple cephalothorax not very unlike that of *Eocarcinus*. *Pithonoton richardsoni* (Text-fig. 1), from the Bajocian (Inferior Oolite), has a comparatively narrow cephalothorax with the rostrum extended in front, the mesogastric lobe completely developed, and a narrow posterior margin. In the later Tithonian forms, the genotype *P. marginatum* (Text-fig. 4) and *P. grande* (Text-fig. 7), the cephalothorax is more foreshortened, the rostrum downturned so that it is not seen in dorsal view, the front widely bilobed, and the posterior margin wider. *P. marginatum* is nearer to *P. richardsoni*, for the mesogastric lobe is completely developed, although not so wide, but in *P. grande* the mesogastric lobe is only indicated by the acutely angular anterior process, and is therefore not even so far developed as it is in *Eocarcinus*. Both in *Eocarcinus* and *Pithonoton* there is a well-developed hepatic lobe in front of the cervical furrow under the lateral margin. But what distinguishes *Pithonoton* is the development of a lateral margin, although it does not extend as far as the branchio-cardiac furrow, and the development of sulci for the eyes, which are deeper in the later Tithonian forms than in the earlier Bajocian *Pithonoton richardsoni*.

The cephalothorax of the Middle Bathonian *Prosopon mammillatum* shows agreement with the more simple *Eocarcinus praecursor* in the absence of sulci for the eyes, the absence of a lateral margin, in the direction of the cervical and branchio-cardiac furrows, and in the presence of the hepatic lobe and a lobe behind what would be the orbital region. In its remaining characters *P. mammillatum* is more advanced, for while in *Eocarcinus* the mesogastric lobe is indicated only by the end of the triangular process behind the rostrum, and by the two short grooves emerging from the cervical furrow, this same lobe is fully developed in *P. mammillatum*, as also are the epigastric and protogastric lobes, and there is a well-developed rostrum.

While some modification has therefore taken place in the cephalothorax of *Prosopon mammillatum* in the direction of the formation of regional lobes, much more rapid and not altogether unexpected development is shown by the abdomen, for it has already the structure of a typical crab. There are no pleura as in *Eocarcinus praecursor*, except in the first two segments, for the outer margins of the third to sixth segments form a continuous line, and the last segment, the telson, is small and acutely angular. Unlike *Eocarcinus*, which has the abdomen extending posteriorly, the abdomen must have to some extent been folded under the cephalothorax, although the lateral excavation of the first two segments shows that these must have been seen in dorsal view, and the last pair of legs were evidently reduced and folded on the back. There are no intercolated plates between the sixth segment and the telson, such as are seen in the later family Dromiidae.

In *Eocarcinus* the last two pairs of legs were reduced and carried on the back. That only the last pair were reduced in *Prosopon* was deduced from the form of the first two segments of the abdomen in *P. mammillatum*, but in the Upper Bathonian *P. auduini* (Eudes-Deslongchamps) and in the Lower Cretaceous (Neocomian) *P. gignouxi* Van Straelen (1928), the 2nd–4th pereiopods appear to be well developed, so that only the last pair could have been reduced.

In short, while *Eocarcinus* shows clearly its derivation from a macrurous stock—the Pemphicoida—*Prosopon* and *Pithonoton* show in turn the derivation of the Prosoponidae from an *Eocarcinus* stock.

Mithracites vectensis, from the Lower Cretaceous (Aptian), as now revealed by its structure, leaves no doubt that it belongs to the family Prosoponidae. *Mithracites* may be regarded as a form derived from the *Prosopon-Pithonoton* stock, for it agrees with both genera in many of its characters. It differs from both genera, which have a more cylindrical cephalothorax with steep sides and concave posterior margin, for the cephalothorax of *Mithracites* is much foreshortened, even sub-circular, it has a wide convex posterior margin, well-defined lateral margins, and the rostrum is not so much downturned and can be seen in dorsal view. It agrees more with *Prosopon*, especially the Middle Bathonian *P. mammillatum*, in the development of the various regions, but the sulci for the eyes are not developed in *Prosopon*; in *Mithracites* the sulci for the eyes are wide and shallow. Although in the Upper Bathonian *P. auduini* (see Withers, 1932, pl. 10, fig. 3) there is no orbital margin developed, there are very slight hollows developed in the orbital region, and these may represent incipient sulci. In the Tithonian species of *Pithonoton* deep sulci for the eyes are present, but in the earlier Bajocian species *Pithonoton richardsoni* the sulci for the eyes are comparatively shallow. In *Prosopon* a lateral margin is not developed; in *Pithonoton* it is only weakly developed anteriorly, for it does not extend as far back as the branchio-cardiac furrow; and in *Mithracites* a lateral margin is well developed.

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—— & Salter, J. W. 1865. See Salter, J. W., & Woodward, H.

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PLATE 15

Pithonoton richardsoni (H. Woodward)

Bajocian, Inferior Oolite, not found *in situ*, but probably from Doulting Beds, *Anabacia* Limestone (= *Clypeus* Grit): Tor Hill, near Wotton-under-Edge, south Cotswolds

FIG. 1. Cephalothorax (holotype). Dorsal view. Brit. Mus., In. 17026.
FIG. 2. Front view of same.
FIG. 3. Side view of same.

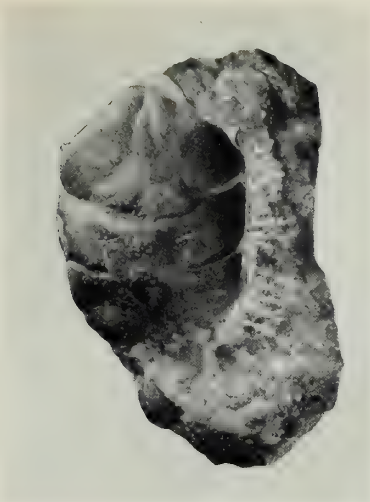
Bajocian, Inferior Oolite, *truelli* sub-zone, Upper Coral Bed: 200 yds. E. of Walnut Farm, Dundry, Somerset.

FIG. 4. Cephalothorax. Dorsal view. Bristol Univ. (Geol. Dept.).

FIG. 5. Front view of same.

FIG. 6. Side view of same.

[Figs. 1–6 × 2 diam. Photographs taken by M. G. Sawyers.]



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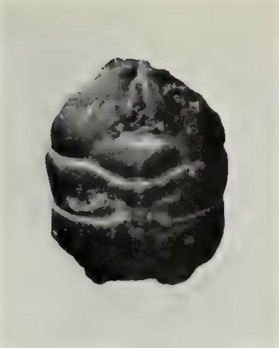

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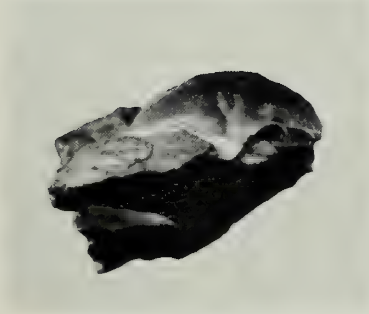

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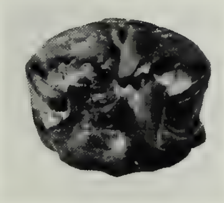

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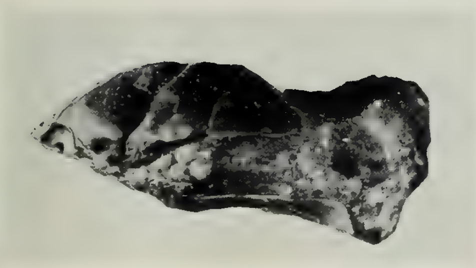

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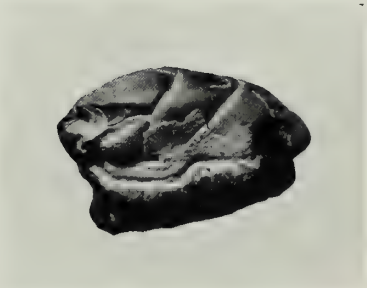

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PITHONOTON RICHARDSONI

PLATE 16

Prosopon mammillatum H. Woodward

Middle Bathonian, Great Oolite, Stonesfield Slate:
Stonesfield, Oxfordshire

Fig. 1. Cephalothorax. Dorsal view. Holotype. Sedgwick Museum, Cambridge, B. 2719.

Fig. 2. Cephalothorax (left half). Brit. Mus., In. 28821.

Fig. 3. Cephalothorax (branchial part of left side). Brit. Mus., I. 269.

Fig. 4. Abdomen (female) of large individual. Brit. Mus., I. 3048.

(Figs. 1–4, nat. size.)

Rathbunopon woodsi n.sp.

Cenomanian, upper *varians* zone (Meyer's Bed 12):
Beer Head, Devonshire

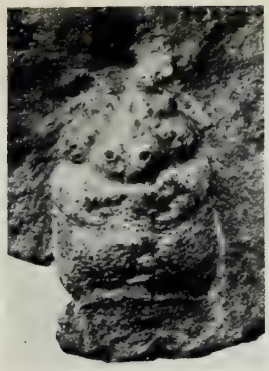
Fig. 5. Cephalothorax (internal cast). Holotype. × 1·5 diam. Sedgwick Museum, Cambridge, B. 50,779.

Fig. 6. Front view of same.

Albian, Gault: Folkestone, Kent.

Fig. 7. Cephalothorax (worn internal cast). × 3 diam. Brit. Mus., 24657.

[Photographs taken by H. G. Herring.]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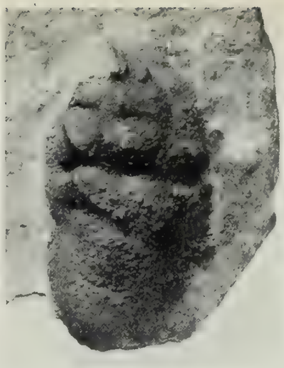
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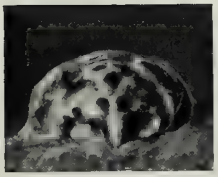
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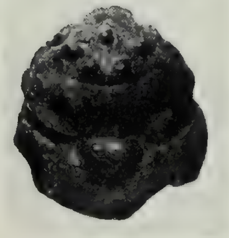
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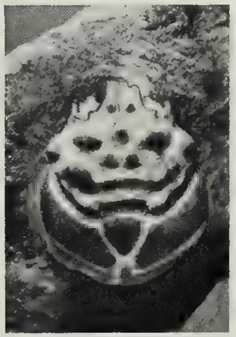
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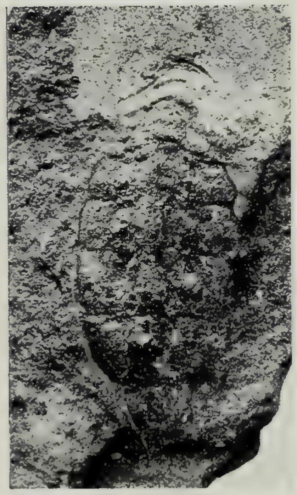
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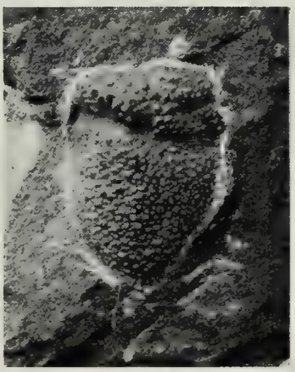
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PROSOPON MAMMILLATUM. (FIGS. 1-4) *AND* RATHBUNOPON WOODSI (FIGS. 5-7)

UM NATURAL HISTORY

PLATE 17

Mithracites vectensis Gould

Lower Greensand (Lower Aptian, *deshayesi* zone): Atherfield,
Isle of Wight

Fig. 1. *a*, Cephalothorax with left cheliped (1st pereiopod); *b*, front view of same showing rostrum and orbital regions; *c*, chela (left) of same. In. 28835.

Fig. 2. *a*, Individual (? female) with right cheliped, and abdomen showing 2nd–5th segments; *b*, part of under surface showing 6th and 7th segments of abdomen (for comparison with male, Fig. 3 *c*). In. 28828.

Fig. 3. *a*, Individual (? male) showing cephalothorax with right eye-stalk, both chelipeds (1st pereiopods), 2nd and 3rd pereiopods (on right side), and 4th pereiopod (on left side); *b*, front view of same showing orbital regions, right eye-stalk, and antennary region; *c*, under surface of same showing buccal-frame, both chelipeds, 4th–7th segments of abdomen, 3rd maxillipede, and 2nd–4th pereiopods; *d*, posterior view of same showing margin, bases of 4th pereiopods, and 2nd segment of abdomen (for comparison with ? female, Fig. 2 *a*). In. 28832.

Fig. 4. Cephalothorax showing under surface with mouth-frame, maxillae, and part of sternum. In 28836.

Fig. 5. *a*, Individual (? male) showing abdomen (2nd–7th segments), 3rd and 4th pereiopods (complete) of right side, and bases of 2nd–4th pereiopods of left side; *b*, dorsal surface of same showing reduced 5th or last pereiopod, elevated on the back. In 25770.

[All figures × 1·5 diam. All the specimens are in the Geological Department of the British Museum. Photographs taken by H. G. Herring.]

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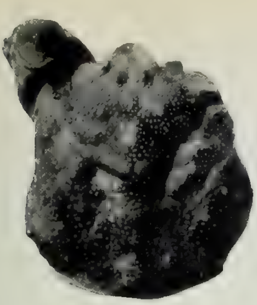

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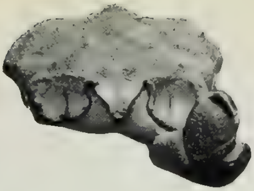

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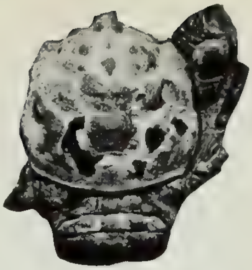

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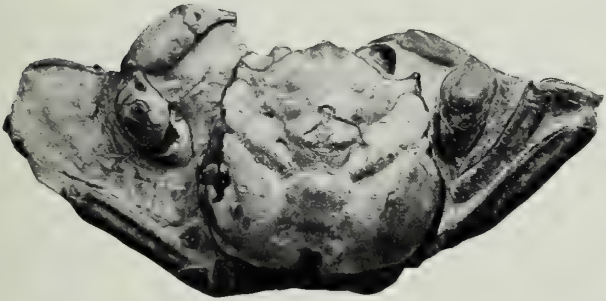
3*a*



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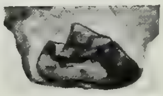
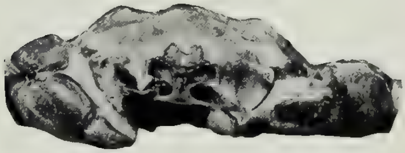


3*d*

3*b*



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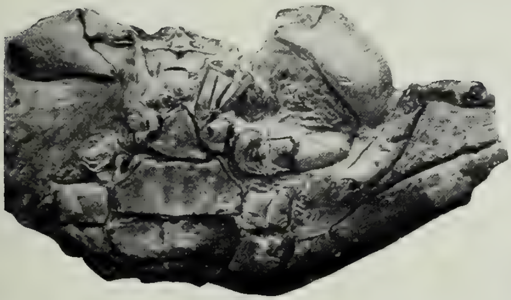

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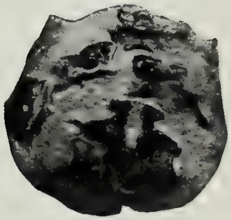

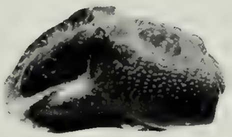

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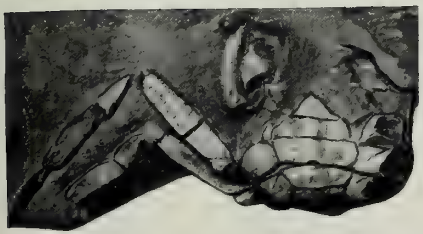
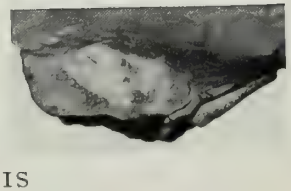


5*a*

5*b*



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BRITISH MUSEUM NATURAL HISTORY

PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
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CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

1 - AUG 1952

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W. N. CROFT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 1 No. 7
LONDON : 1952

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BY

WILLIAM N. CROFT

BRITISH MUSEUM NATURAL HISTORY

Pp. 187–220; Pls. 18–19; 7 Text-figures

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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A NEW *TROCHILISCUS* (CHAROPHYTA) FROM THE DOWNTONIAN OF PODOLIA

By W. N. CROFT

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SYNOPSIS

Trochiliscus (*Eutrochiliscus*) *podolicus* n.sp. is described from beds of Lower Devonian (Downtonian) age from the Podolian of eastern Europe. It is the earliest species of the genus and the earliest Charophyte of which there is reliable evidence. The fruits are unusually well preserved and permit detailed comparison to be made with the lime-shell, oospore membrane, and oospore contents of Recent and fossil Charophytes. The fresh evidence amply confirms the Charophyte affinity of the genus. The classification of *Trochiliscus* is discussed and the species are grouped into two new sub-genera, *Eutrochiliscus* and *Karpinskya*. It is concluded from a review of the geological occurrences of *Trochiliscus* and *Sycidium*, and from the nature of their oospores, that they were probably land-plants, growing, like the Recent Charophyta, in fresh or brackish water.

The structure of the Oligo-Miocene species *Chara escheri* is found to agree in detail with that of living *Chara*.

I. INTRODUCTION

The fossils placed in the genus *Trochiliscus* differ from post-Lower Carboniferous and Recent charophyte fruits in that the spiral enveloping cells number more than five, and have a right-hand, not a left-hand, twist. They were first discovered nearly 100 years ago in the Devonian of north-west Russia, and were later recognized in the same formation in North America. During the latter half of last century they were assigned to groups in both the plant and animal kingdoms, especially the Foraminifera. Quenstedt (1867:843) was one of the first to compare these bodies with charophyte fruits. A few years later the first American examples were described by Meek (1873) as probably the fruits of *Chara*. But it was not until the appearance of Karpinsky's admirable and elaborate monograph in 1906, which was based on the European trochilisks[1]—*Trochiliscus* and *Sycidium*—that sound reasons were given for placing these genera in the Charophyta. This view was not, however, generally accepted, and it was left to Peck in 1934, as a result of a detailed study of the North American species of *Trochiliscus*, a study which proved as fruitful as Karpinsky (1907) had predicted, to provide convincing evidence that this genus was correctly placed in the Charophyta. That evidence—particularly the discovery of species with calcified coronula cells—is now supplemented by a fuller knowledge of the structure of the fruit given by the unusually well-preserved remains of a new species from eastern Europe.

---

[1] Pander (1856: 17; 1857: 13) and all later writers in German use the vernacular term *Trochilisken*. Karpinsky (1907: 123) also uses the French *trochilisques*. Hecker (1941) writes *trochilisks*, and this is presumably the correct form in English.

The interest of the trochilisks lies partly in the fact that they are the most typical calcareous Algae of the Devonian period, and partly in the evidence they give of the very early adaptation of marine Algae to fresh- or brackish-water conditions.

Grateful acknowledgements are made to all those who have assisted in the preparation of this paper: to Mr. G. O. Allen for valuable discussions on problems relating to living charophytes and for the loan of Recent material; to Prof. W. H. Lang for criticism and advice; to Prof. T. M. Harris for helpful discussions; to Mr. W. N. Edwards for advice and encouragement; to Mr. F. M. Wonnacott for help, especially with the bibliography; and to Mr. J. E. Owen for much practical assistance.

Prof. R. E. Peck has very kindly read through the paper and made some valuable suggestions.

II. LOCALITIES AND HORIZONS OF *TROCHILISCUS*

The specimens of *Trochiliscus* and *Sycidium* in the Pander and Volborth collections described by Karpinsky (1906: 107) came mainly from the neighbourhood of Pavlovsk, which is 30 km. south-south-east of Leningrad. Localities in Esthonia, Dorpat (now Tartu) and Isborsk (now Irboska), were also mentioned. In the Baltic States, and in the Leningrad and Kalinin areas of Russia, not only is the whole of the Lower Devonian missing, but also the basal part of the Middle Devonian. Recent Russian work, summarized by Hecker (1941: 75 et seq.), shows that the Leningrad localities occur in the two lowest of the four stratigraphical divisions of the Middle Devonian of the Main Devonian Field, in beds resting unconformably on planed Cambrian and Ordovician rocks. These divisions, the Pärnu and Narova beds, which are assigned to the Upper Middle Devonian (Givetian) by Jarvik (1949: 42), contain abundant trochilisks, whereas none appear to be present in the two overlying divisions. Trochilisks are also stated to occur in local abundance in certain divisions of the Upper Devonian, but *Trochiliscus* is not mentioned by name and the reference is probably to *Sycidium*. In Esthonia trochilisks, presumably both *Trochiliscus* and *Sycidium*, occur in the same Middle Devonian beds as in the Leningrad area, and have given their name to the 'Trochilisken-Sandstein' (Orviku, 1930). This recent work amplifies Karpinsky's general statement that the Russian trochilisks were obtained from beds belonging to the Middle, and the lower part of the Upper, Devonian (Karpinsky, 1906: 114).

The North American material described by Peck (1934, 1936) came from several localities and horizons of Devonian and basal Mississippian age. The youngest horizon, the Sylamore sandstone of central Missouri, is now known as the Bushberg sandstone (Branson, 1944: 176, 185). The oldest specimens, with the possible exception of those from the shale below the Mineola limestone, are from the Jeffersonville and Columbus limestones of Onondaga age, which are placed by Cooper *et al.* (1942) in the uppermost Lower Devonian (Coblentzian) of the European succession.

More recently, *Trochiliscus* has been obtained in cores from 'near the base of the Onondaga formation' in south-west Ontario, Canada (Fritz, 1939). Dr. Fritz has kindly informed me (*in litt.*, September 1950) that this material has not been described.

Lastly, some minute, more or less spherical, calcareous bodies have been described from the Devonian of Texas, U.S.A., as 'questionable internal molds of trochiliscid oogonia' (Ellison & Wynn, 1950: 795, pl. 1, figs. 1–7). The horizon is uncertain, but a Lower Devonian age is possible. The bodies are associated with conodonts and fish-remains in a basal glauconitic sandstone resting on strata assigned to the Silurian.

The Russian, Esthonian, and North American localities have provided all the known material of *Trochiliscus*. The species described below is from a new area, west Podolia, on the borders of Poland and Russia. The specimens were found by Mr. H. A. Toombs in the rock matrix of the W. Zych collection of fishes which was acquired by the British Museum (Natural History) in 1935. They came from fish-beds in the Czortkov series of the Downtonian of Podolia and are labelled 'Polen. Podolien. Jagielnica [or Jagielnica Stara]. Old Red.' The town of Jagielnica (lat. 48° 57′ N.; long. 25° 45′ E.) is 150 km. south-east of Lvov and 16 km. south-west of Czortkov. Jagielnica Stara is 5 km. south-south-east of Jagielnica. Dr. Zb. Sujkowski-Leliwa informs me that in this area the Czortkov series has a very gentle dip to the west, is unfaulted, and that the beds at these two places are therefore at approximately the same horizon. This is supported by the lack of any obvious lithological difference in the matrices and by the identity of the *Trochiliscus* remains from the two localities. The majority of the specimens described below are from the Jagielnica locality.

The age of the fish-beds is accurately determined as early Lower Devonian (Downtonian = lower Gedinnian). Stensiö (1944: 4, footnote) records *Corvaspis* in the fish fauna from Jagielnica Stara and correlates these uppermost beds of the Czortkov series with the late Downtonian strata in England and Spitsbergen in which this genus occurs. According to the zonal classification of White (1950: fig. 1), *Corvaspis* is restricted to the highest beds of the Downtonian (Lower Old Red Sandstone) in the Anglo-Welsh area. (See also Westoll (1951) for detailed correlations of the European Devonian.) It is certain therefore that the Podolian *Trochiliscus* is older than the previously described species from Russia and North America; and, unless the Silurian age of '*Pseudosycidium*' from Turkestan (Hacquaert, 1932) should be confirmed, it is the earliest charophyte of which we have reliable evidence.

III. MATERIAL AND METHODS

The pale buff-coloured matrix containing the fossil fruits consists of siltstone with harder layers of fine calcareous sandstone. The fruits, all of which belong to one species, are conspicuous on weathered and broken surfaces as shown by specimens V.27158–V.27171.[1] Their preservation is unusually good. The outer shell consists of cloudy or banded calcite without silicification, and remains of the organic contents are preserved in the clear crystalline calcite which fills the central cavity. Deposits of pyrite or reddish-brown granular mineral (which are readily distinguishable from carbonaceous material by reflected light) are sometimes present in the central cavity and in the apical or basal openings.

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[1] The registered numbers refer to specimens in the Geol. Dept., British Museum (Natural History).

The abundant material was studied by the following methods. Harder layers, in which the fruits comprise perhaps 20 per cent. of the rock by bulk, were made into thin ground sections which gave useful information as to the morphology of the gyrogonite. Most of the work, however, was done on material isolated from the matrix.

The siltstone breaks down when boiled for several hours in dilute sodium carbonate solution and the fruits can be concentrated by washing, and cleaned with a sharp needle on a glass slide coated with plasticine. Several hundred specimens were extracted from a few cubic centimetres of the rock and, as Pander wrote of the Leningrad material, could no doubt be obtained 'by the bushel'. Many of them show some degree of distortion attributable to compaction of the sediment. The external measurements of the gyrogonites given below were obtained from about 100 specimens all of which showed spiral ribbing. A few of the gyrogonites which have no spiral ornament and do not at first sight seem to belong to the normal form owe their different appearance to corrosion. Vertically ribbed or pitted bodies which could be attributed to *Sycidium* are absent.

No vegetative axes of the parent plant, such as those which were associated with the Russian trochilisks (cf. Karpinsky, 1906: figs. 46–57), have been found with the fruits.

Examination and photography of these minute bodies were greatly assisted by whitening them with a thin deposit of ammonium chloride by means of the simple but effective apparatus described by Teichert (1948). The deposit being much heavier on the ridges than in the furrows, the ridges become more strongly emphasized.

In order to obtain mounts of the delicate organic contents of the fossil gyrogonites, the bodies were gently dissolved in 1 per cent. HCl and the insoluble remains were transferred direct to gum chloral by pipette, without further treatment, and covered.

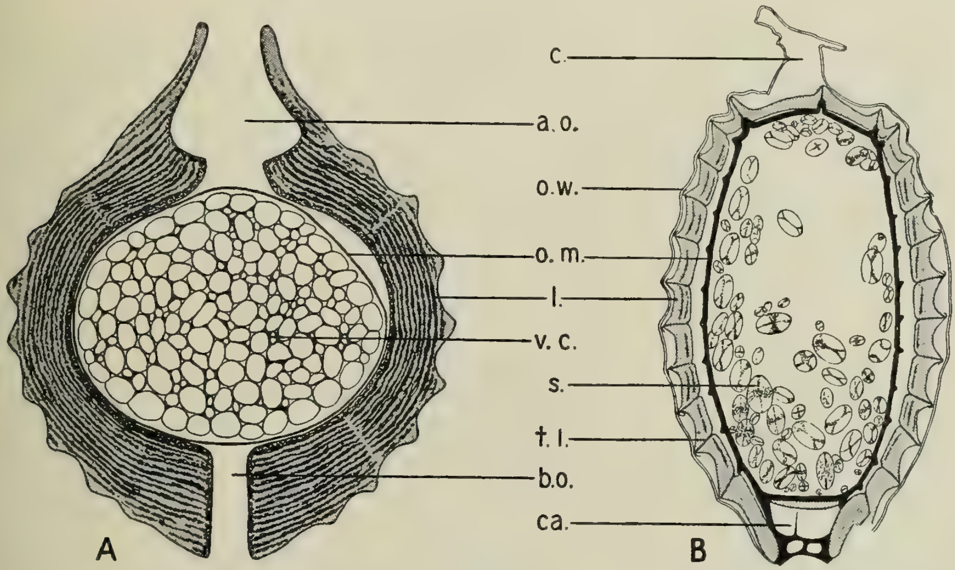
Ground sections of the isolated gyrogonites were made by first embedding them, either singly or in groups, in the transparent plastic, 'Marco' resin (Purves & Martin, 1950). Sections of the gyrogonites of Recent and fossil Charas were made in the same way.

IV. DESCRIPTION OF THE MATERIAL

The terminology of the following description is mainly that adopted by Peck (1934: 104). Harris (1939: 12) in reviving the term *gyrogonite* pointed out that 'it is not quite accurate to term the calcareous body found fossil the "oogonium", as most authors do, since it is but the calcareous inner part of the oogonium' (using the latter term to mean the egg-cell together with its sheath of sterile enveloping cells). The term *gyrogonite*, which may well be used to include all fossil charophyte fruits irrespective of the number and direction of the enveloping cells, is accordingly used here in preference to *oogonium*. The phrase 'gyrogonite non-coronulate' may then be employed without prejudice to the view that the female organ probably had a coronula which left no trace on the gyrogonite, either because it was minute or deciduous, or because it was never calcified. The term *oogonium* is in any case liable to be misunderstood for, as used by German authors, it generally applies to the egg-cell alone, which is the only part of the female organ that is homologous with the oogonium in other Algae (see Moll, 1934: 117; Smith, 1938: 130; Wood, 1947: 241; Fritsch, 1935). *Egg-bud*, the English equivalent of Sachs's term *Eiknospe* (see Oltmanns, 1922: 449)—an unexceptionable name for the female organ—has only recently been introduced (Maslov, 1947).

The term 'lime-shell' (Groves & Bullock-Webster, 1920: 74) is used for the calcareous wall of the fruit. It encloses the thickened oospore membrane (*Hartschale*) which in turn encloses the mature ovum. The terms *cellular* and *intercellular*, as applied to the sculpturing of the lime-shell, have been defined by Peck (1934: 104).

The use of these and other terms is illustrated in Text-fig. 1.



Text-fig. 1. A. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. L. Devonian. Restoration of gyrogonite in median longitudinal section. × 120. B. *Chara hispida* L. Fruit of Recent species in median longitudinal section in polarized light. × 70. (V.28356.) Cf. Groves & Bullock-Webster (1924: pl. 31, fig. 6).

a.o., apical opening; *b.o.*, basal opening; *c.*, shrivelled remains of coronula; *ca.*, cage, enclosing the winding cell, node-cell, and (?) stalk-cell; *l.*, lime-shell; *o.m.*, oospore membrane; *o.w.*, outer wall of fruit; *s.*, starch-grains, many of which have fallen away; *t.l.*, thickened lateral walls of spiral cells; *v.c.*, vesicular contents. The furrows on the lime-shell of *Chara*, and probably of *Trochiliscus*, are *cellular*, and the ridges *intercellular*.

CHAROPHYTA

Family TROCHILISCACEAE

Genus ***TROCHILISCUS*** Karpinsky 1906

Grounds for rejecting the name *Calcisphaera* and for attributing the authorship of the genus to Karpinsky are given by Peck (1934: 105). The status of the problematical Carboniferous genus *Calcisphaera* Williamson has been discussed by Pia (1937: 803). In spite of imperfect figuring and description it is almost certain that *Moellerina greenei* Ulrich is a *Trochiliscus*, probably conspecific with *T. devonicus* from the same locality (see below, p. 206). Should this be confirmed on the discovery of the type material, a case could be made for conserving the comparatively well-known name *Trochiliscus*

Sub-genus EUTROCHILISCUS nov. (see p. 209 below)

Trochiliscus* (*Eutrochiliscus*) *podolicus n.sp.

(PL. 18; PL. 19, FIGS. 17–19; TEXT-FIGS. 1–4)

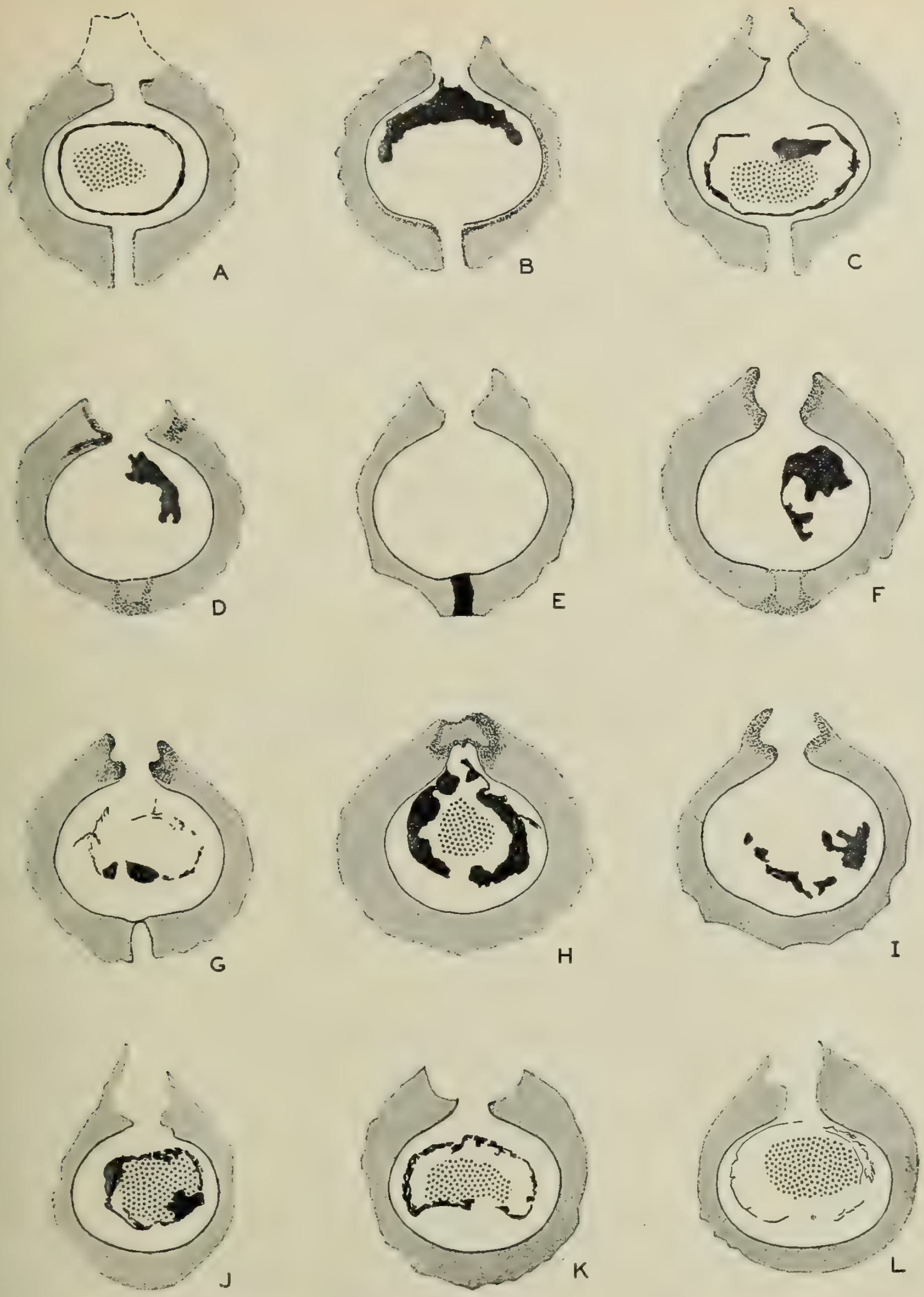
DIAGNOSIS. Gyrogonite non-coronulate, bulbiform; diameter 530 μ ± 20 per cent.; length including apical beak 580 μ ± 20 per cent. Ridges 10, making rather more than a complete turn round gyrogonite, moderately sharp with rounded furrows between; equatorial angle approximately 20°; about 10 to 12 ridges seen in lateral view. Apical opening expanded in middle part, proximally about 60 μ wide. Basal opening cylindrical, about 40 μ in diameter. Lime-shell concentrically laminated with *c.* 3–5 μ spacing between bands. Oospore membrane very thin (1 μ), generally brown and translucent with fine granulate decoration.

HOLOTYPE. V.28340. Geol. Dept., B.M. (N.H.).

LOCALITIES AND HORIZON. Jagielnica and Jagielnica Stara, west Podolia. Fish-beds in Czortkov series; Lower Devonian (Downtonian).

DESCRIPTION: *General Morphology*. The somewhat variable shape and size of the gyrogonite in lateral view is indicated in Pl. 18, figs. 1–5, and Text-fig. 2. Pl. 18, figs. 4 and 5 are examples of specimens with a pronounced apical beak. In the majority of specimens, however, the beak is poorly developed, either because it was originally incompletely calcified, or because it was subsequently broken off. The base of the gyrogonite is rounded, or slightly produced (Pl. 18, figs. 6, 7). Out of 100 specimens measured, 97 were found to have a breadth of 530 μ ± 20 per cent., and 90 an overall length of 580 μ ± 20 per cent., the remainder lying just outside these ranges. The size variations are shown in the frequency diagrams in Text-fig. 4.

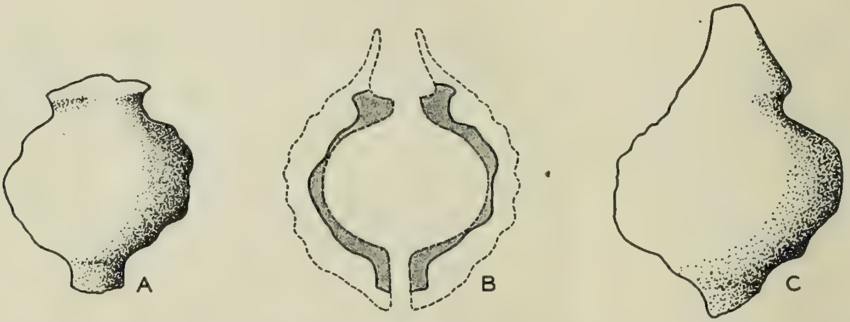
The dextrally spiralled ridges are moderately sharp with rounded furrows between. The prominence of the ridges may vary on different areas of the same specimen, due to incomplete removal of the matrix or to abrasion. In Pl. 18, figs. 1–5 the ridges appear blunted due to the somewhat granular coating of ammonium chloride. In thin sections of the rock the outline of the lime-shell is often indefinite (Pl. 18, fig. 8) and the ridges and furrows are usually less well shown than by some of the sections of isolated specimens (Pl. 18, fig. 7). The equatorial angle of the ridges varies from about 17° to 24°. The ridges make approximately 1¼ turns round the gyrogonite, and, on passing on to the beak, become sub-parallel to its axis (Pl. 18, figs. 4, 5). It is usually possible to count 10 to 12 ridges in lateral view. In only 11 specimens was the base well enough preserved to allow the number of ridges to be counted with certainty. These all showed 10 ridges springing from a small basal opening. They are clearly seen in the holotype, Pl. 18, fig. 2.



Text-fig. 2. A–L. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Somewhat diagrammatic drawings of gyrogonites in approximately median longitudinal section. All ×60. Light tone = lime-shell; dark tone = oospore membrane; stippling = remains of oospore contents. (A–E, V.28348; F, V.28351; G–K, V.28349; L, V.28350.)

The apical and basal openings are often marked by a zone of brown staining in the surrounding lime-shell, as indicated by shading in Text-fig. 2. This staining, which contrasts with the light-coloured matrix filling the openings, may be seen in sections, and in surface view when the gyrogonite is immersed in xylol. In median longitudinal sections (Pl. 18, figs. 6, 7) the basal opening is more or less cylindrical with a maximum length of about 140 μ; in surface view under xylol it is circular in section with a diameter of about 40 μ (20 μ–60 μ).

The apical opening differs in shape and size from the basal opening. This is well seen in Pl. 18, figs. 6 and 7, especially the first, which shows both openings filled with dark material. Traced outwards the apical opening at first decreases more or less rapidly to a diameter of approximately 60 μ, and then expands rather suddenly to nearly three times this width: thereafter the diameter slowly decreases until the apex of the beak is reached (Text-fig. 2J). The lime-shell becomes thin where the opening reaches its greatest diameter, and the apex is often broken off along this line of weakness. This description is supported by the examination of specimens in surface view, for the ends of the more prominent beaks are only about 100 μ across, or somewhat less, and in these the opening at the tip does not exceed a diameter of 75 μ. The opening is, however, considerably larger when the beak is missing. The rather variable appearances of the apical opening as shown in Text-fig. 2 may be explained by the degree of obliquity[1] of the sections; by more or less incomplete preservation of the beak; or by individual variations. The clear calcite of the central cavity usually extends into the narrow part of the opening, the expanded portion being filled with matrix.



TEXT-FIG. 3. A–C. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Corroded gyrogonites. In B, the relation between the corroded and the normal forms is indicated diagrammatically. (A, V.28593; C, V.28594. × *c*. 60.)

The corroded gyrogonites (Text-fig. 3) are, on the average, decidedly smaller. The degraded beak is often delimited from the body of the gyrogonite by a shallow groove giving the gyrogonite a rather distinctive appearance. There may also be a small, but prominent, basal projection. A few specimens with these characters have been detected in thin sections of the rock.

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[1] Cf. Pia (1936: 45) on the differing appearances of random sections through short cylinders.

Sections of the gyrogonites show an outer cloudy or dark zone—the lime-shell—which is sometimes closely banded, and an inner mass of clear calcite occupying the central cavity. The organic contents preserved in the calcite comprise a contracted organic membrane, interpreted as the original oospore membrane; and within this a brownish mass, sometimes showing a well-marked vesicular structure, which is regarded as the remains of the ovum. The organic contents appear as a dark patch when the gyrogonite is immersed in xylol. The granular nature of the lime-shell is indicated by the fact that thin sections remain illuminated throughout a complete rotation between crossed nicols. The clear calcite filling the central cavity, on the other hand, consists of a few large crystals which may be partially bounded by the contracted oospore membrane. The lime-shell, oospore membrane, and vesicular contents will be described in turn.

Lime-shell. The thickness of the lime-shell at the equator varies from about 40 μ to 70 μ, but in a few specimens it is much thinner. The inner surface is smooth without ribs or furrows. In sections of the majority of specimens the lime-shell appears to be structureless. In others there is a more or less definite indication of a concentric layering or lamination, which is clearly demonstrated in a few well-preserved specimens. Thus the specimen in Pl. 18, fig. 9, part of which is enlarged in Pl. 18, fig. 10, shows a concentric banding of light and dark laminations. They are still more clearly marked in Pl. 18, fig. 11, which also shows that they may end abruptly in a structureless portion of the lime-shell. The spacing of the dark laminations in different specimens is remarkably constant, ranging from 3 μ to 5 μ. In the two specimens figured and in others the layers are only slightly rippled. In none of the numerous sections examined is there any undulation at all comparable in amplitude or wave-length with that of the ridges or furrows. In Pl. 18, fig. 12 the indistinct layering appears to be more or less concentric and certainly does not reflect the strong undulations of the ridges and furrows. There are few indications of radial interruptions in the layering, and these are too irregularly spaced to suggest the positions of the lateral walls of spiral enveloping cells.

Oospore membrane. A contracted continuous membrane, often broken up by numerous cracks and considerably disrupted, is present in most, if not all, of the gyrogonites. A good example of a membrane in approximately optical section is shown in Pl. 18, fig. 7; others are represented in Text-fig. 2. Under high power the membrane is found to be very thin, and is uniformly about 1 μ thick. Because of the clearness of the calcite, the membrane appears much thicker in oblique optical section, and is thus represented in some of the drawings in Text-fig. 2. The specimen in Pl. 18, fig. 8 is unusual in that the membrane is double as though an inner and an outer layer had separated. The outer layer is somewhat thicker and darker than the inner; but their combined thickness does not exceed 1 μ. The contraction of the membrane is usually greater away from the basal end of the gyrogonite, and the displaced membrane sometimes projects towards, or even extends into, the expanded portion of the apical opening. The symmetrical structure in Pl. 18, fig. 14, however, is not a mere projection of the oospore membrane but a distinct 'appendage' with a thinner and more translucent wall. A simple explanation of it would be that it is a contracted membrane which lined the lower part of the apical opening and did not become involved in the thickening of the oosphere wall. It has not, however, been observed in any other specimen.

The membrane is readily isolated by decalcification of the gyrogonite and its characters are then studied more easily. Sometimes the more or less globular shape is retained (V.28557). The membrane is usually translucent and pale to dark brown by transmitted light, but it may be black and opaque. The more translucent membranes are decorated with small irregular granules, as in Pl. 19, fig. 17, which is magnified × 500. A similar, but coarser, decoration, seen in Pl. 19, fig. 18 at the same magnification, is exceptional. A few of the membranes examined have scattered (sometimes contiguous), more or less circular, thicker areas, about 3–5 μ in diameter, some of which have a minute central pore. Examples of these thickenings, which are sometimes partially torn away from the membrane, leaving a rent, are shown in Pl. 19, fig. 19. None of the membranes has any parallel ridges or lines on its surface.

Vesicular contents of oospore. In ground sections of many specimens the brown contents lying within the oospore membrane resemble patches and wisps of disorganized tissue. Others show a definite cellular pattern, as in Pl. 18, fig. 14. Pl. 18, fig. 13 is a section showing a distinct, rounded margin to the vesicular body. In this, as in most other specimens, the contents have undergone greater contraction than the enveloping membrane. The best demonstration of the vesicular structure and of the globular form is afforded by decalcified specimens. Pl. 18, fig. 15 shows one of the spherical bodies, 240 μ in diameter, still enclosed within the partially ruptured oospore membrane. In Pl. 18, fig. 16 a similar specimen, freed from the membrane, is shown at a higher magnification. The rather uniform, frothy tissue is made up of rounded vesicles, which are frequently oval in optical section. The outer walls of the vesicles are convex, and there is no evidence that the vesicular mass had its own investing membrane. In these two examples the major axes of the vesicles measure about 25 μ; in less contracted specimens they may reach 40 μ.

DISCUSSION. This species is distinguished from *T. ingricus* by the much smaller number of spiral ridges; and from *T. bulbiformis*, which it resembles in shape, by its greater size (diameter about 530 μ compared with 250–400 μ). The number of ridges is also different, being 10 instead of 8 or 9. It differs from the North American species *T. convolutus* (*T. minutus* and *T. multivolvis*) in the much greater convolution of the ridges (360°+ compared with 180°+), and it is also somewhat larger (average diameter 530 μ compared with 300–400 μ). Disregarding the doubtful forms *T. lemoni* and '*Moellerina greenei*', *T. podolicus* is the most convolute *Trochiliscus* known.

Karpinsky showed that his species *T. ingricus* normally had 18 spiral ridges, corresponding to 18 spiral cells. From analogy with some American specimens which have two ridges in each cell, Peck (1936: 765) concluded that there were probably only 9 spiral cells. If this were so, 18 ridges or furrows on the outside of the lime-shell would correspond to 9 ridges or furrows on the inside of the shell. But Karpinsky's figures of a section through the gyrogonite show 18 ridges and furrows on both the inner and outer surfaces (Karpinsky, 1906: pl. 2, fig. 28; text-fig. 31). Sections made of topotype material kindly loaned by Prof. T. G. Halle from the Riksmuseum Collections confirm Karpinsky's figures. Owing to the steepness of the spirals an equatorial section cuts all the ridges almost at right angles. The meeting of a pair of ridges in a V near the pole is not in itself evidence that both ridges belong to one cell (see, for example, Peck, 1934: pl. 10, figs. 23, 24).

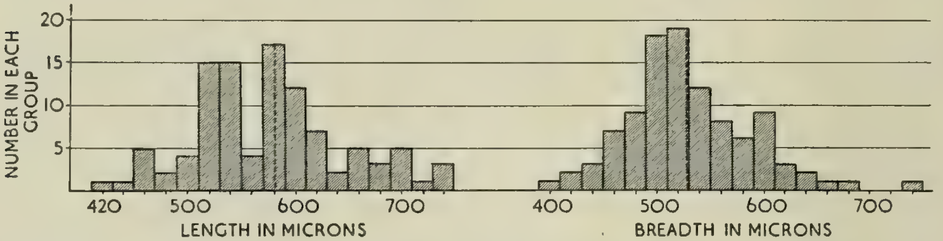
Only limited comparison is possible between the relatively well-preserved internal structures of *T. podolicus* and those of other species. It is not known whether the expansion of the middle part of the apical opening is a feature of other non-coronulate species, but coronulate species have a funnel-shaped opening (Peck, 1934: pl. 11, fig. 19). Although direct evidence of the cellular nature of the lime-shell is lacking in *T. podolicus*, the spiral ridges are presumably intercellular, as in the Russian species of *Trochiliscus*. The absence of furrows on the inner surface of the lime-shell, of regular radial interruptions in the concentric layering, and of ridges on the oospore membrane, may all be explained by non-induration of the radial walls of the spiral cells. A similar continuity of the lime-shell is presumably found in those Recent fruits which have oospore membranes with only faintly marked spiral ridges.

The layering of the lime-shell has not been clearly demonstrated in other species of *Trochiliscus*, few of which have been sectioned. Peck's sections of coronulate gyrogonites show a strongly concave, sometimes U-shaped or V-shaped, dark band in each transversely-cut spiral cell. These bands, which are apparently without stratification, much resemble those found in *Clavator* and *Perimneste* (Harris, 1939: 64, pl. ix, fig. 3). It may perhaps be doubted whether the bands represent the structure or layering in its original form, for the original lime-shell in all these specimens has been replaced by silica. There is, on the other hand, very close agreement between *T. podolicus* and *Sycidium* in the layering of the lime-shell, as Karpinsky's (1906: 105) detailed description and clear figures show. The only notable differences are that in *Sycidium* the banding is often regularly concave and thereby reveals the original cellular structure; and that the spacing of the bands is more than twice as great: Karpinsky gives an average of 11 μ, which compares with 3–5 μ in *T. podolicus*. This difference in spacing is matched by the greater size and thickness of the *Sycidium* shells which have been figured.

Remains of the contents of the oospore have not previously been described, but the oospore membrane has been recorded from Europe and America. Karpinsky (1906: 157, text-fig. 58), in sections of trochilisks identified as *Sycidium*?, found that there were 'unverkennbare Spuren ihnen anhaftender vegetabilischer Membran' lining the inner surface of the lime-shell. He considered that this was very like the corresponding membrane in the Characeae. Peck (1934: 91, 98) recognized the oospore membrane in coronulate and non-coronulate specimens of *Trochiliscus* and also in *Sycidium*. His specimens are silicified and the membrane is preserved as a thin layer, or 'inner sphere of white cryptocrystalline silica', which is often contracted and folded, but is sometimes in contact with the lime-shell. A few of his sections, e.g. pl. 11, fig. 23, suggest that the original organic substance has not been completely replaced. For both *Trochiliscus* and *Sycidium* he described the membrane as an 'inner sac . . . suspended from the summit opening' (Peck, 1934: 95, pl. 11, fig. 13; pl. 13, fig. 16). This rather unusual appearance may be due to the contraction of the closed membrane away from the sides and base of the lime-shell, and its extension by displacement into the apical opening (cf. Text-fig. 2H).

V. CHAROPHYTE AFFINITIES

It is unnecessary to restate the morphological considerations which led Karpinsky, and later Peck, to postulate the affinity of *Trochiliscus* with the Charophyta. Perhaps the most convincing evidence was Peck's demonstration that several North American species of *Trochiliscus* had apical structures, corresponding in number and position with the spiral cells, which could readily be interpreted as the cells of a calcified coronula. The present study of a new species of *Trochiliscus* has provided increased knowledge of the structure of the fruits, and the following detailed comparison with Recent and fossil charophytes confirms and strengthens this affinity.



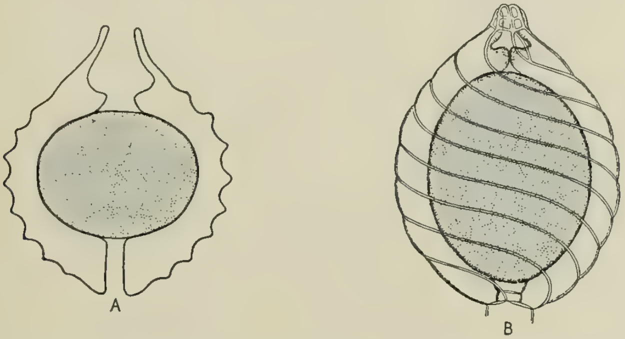
TEXT-FIG. 4. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Histograms showing the size frequencies of 100 gyrogonites.

Size variation. There is an interesting and surprisingly close agreement between the size variations of the gyrogonite of *T. podolicus* and the equivalent measurements for the Recent *Chara vulgaris* and the Purbeck charophytes. Harris found that over 99 per cent. of a batch of 500 spores (oospores) of *Chara vulgaris* had lengths between the limits 610 $\mu \pm 20$ per cent. He found the same variation in the spore diameters, nearly all of which lay within ± 20 per cent. of a mean. Similar results were given by Purbeck charophytes. The corresponding figures for *T. podolicus* are 97 per cent. (breadth) and 90 per cent. (length). The loss of the beak in many specimens is no doubt responsible for the greater variation in length, while the breadth measurements are affected, though to a lesser extent, by distortion of the specimens through compression. The variations are represented graphically in Text-fig. 4, which may be compared with Harris's text-fig. 16.

Lime-shell. The importance of the charophyte lime-shell needs no emphasis; yet no systematic study of its structure has been made. It is generally the only part of the plant preserved as a fossil, which is no doubt due to the special manner of its formation. In the calcareous Algae generally, and on the vegetative parts of many charophytes, lime is deposited as minute crystals in the mucilage surrounding the cell-walls (Fritsch, 1950: 62). The gyrogonite is exceptional in that the lime composing it is laid down in the interior of the enveloping cells and may largely replace their protoplasmic contents. An appreciable amount of calcium succinate, a soluble salt of calcium, is present in the cell-sap of *Chara* (Davis, 1901: 504).

The small basal opening in the gyrogonite of *T. podolicus* agrees generally with the equivalent opening in Recent and fossil charophytes. The lime-shells of recent

Chareae lack an apical opening, but it is present in some fossil species, and in the Purbeck Charophyta. As Karpinsky (1906: 130, 151) has pointed out, there is an opening between the distal ends of the uncalcified enveloping cells in young stages of *Nitella*. At maturity, if the coronula is dehiscent, antherozoids can pass directly into this opening, which is termed the 'neck-canal' by Migula (1897: 46). If the coronula is persistent, antherozoids enter the 'neck-canal' through slits between the enveloping cells. The 'neck-canal' may either be expanded distally, as in *Chara vulgaris*; or medially, as in *Nitella tenuissima*, when it much resembles the apical opening in *T. podolicus* (Text-fig. 5). See also Groves & Bullock-Webster, 1920: fig. 22, ii. The expanded portion is termed the *Scheitelraum* by de Bary (1871).



TEXT-FIG. 5. A. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. L. Devonian. Gyrogonite in median longitudinal section. ×*c*. 55. B. *Nitella tenuissima*. Recent. Mature fruit. ×*c*. 90. After de Bary (1871).

The similarity of the layering of the lime-shell of *Sycidium* and *Chara* has already been noted by Karpinsky (1906). His pl. 3, fig. 14 shows a section of the lime-shell of a Miocene '*Chara*' cut parallel to the ridges, and he observes that the spacing of the light and dark bands is about the same as that of the finest layers in the shell of large species of *Sycidium*. A few of the gyrogonites of *C. hispida* sectioned for this paper show a faint but definite banding in places, the bands being about 4 μ apart, as in *T. podolicus*. Layering is much better shown by a gyrogonite of the fossil *C. escheri* (Pl. 19, fig. 28), although little or no indication of layering is given by the other 50 specimens on the same slide. The dark, more or less concentric, lamellae have an average spacing of about 3 μ. The uniformity in the character and spacing of the layering in these lime-shells, allowing for the greater size of *Sycidium*, strongly suggests that the banding is an original feature of the lime-shell.

Karpinsky (1906: 129) ascribed the growth of the lime-shell to the layering of calcium carbonate particles within a mucilaginous or gelatinous substance. Layered concretions have been produced artificially by several workers by the precipitation of salts in the presence of organic colloids (Carpenter, 1901: 1100). Through the work of Schade much light has been thrown on the principles involved and on the relations between the visible structure of concretions, their composition, and the conditions under which they are formed. The lime-shell appears to be a good example of what Schade has termed *concrement formation.* He postulates that concrements, such as gallstones and ooliths, are built up in layers by the apposition of colloid and crystalloid particles. 'Precipitating colloids . . . produce a concentric layered structure, while crystalloids favour a radial striation. Where large percentages of both constituents appear, both types of structure coexist, interwoven' (Schade, 1928: 823). Ooliths, like the great majority of concrements, are composed of both crystalloids and colloids. When an oolith is treated with acid, the calcium carbonate (crystalloid) is dissolved and a distinct skeleton of silicic acid (colloid) remains. The lime-shell behaves in the same way. It has long been known that on removal of the lime the shell is represented by a delicate and closely stratified membrane (de Bary, 1875: 301). Migula (1897: 49) observed in thin sections of the shell that the delicate lamellae separating the calcareous layers were not destroyed by the acid, and concluded that they were possibly gelatinous. And Nordstedt (1889: 3) found that silicic acid was present in the oospore membrane. This substance may therefore be a constituent of the colloidal element in the lime-shell, as in ooliths and other calcareous concrements.

The close comparison between the structure of the layered lime-shell of the trochilisks and that of gallstones and ooliths showing secondary crystalline formation may be seen by examination of Schade's figs. 35, 36, 54, and 55. These figures show in places a very similar radial obliteration of the layering, due to transformation of the calcite, i.e. the growth of some crystalloid particles by the absorption of others. They also show indications of a radial striation; the breaking up of the dark bands into discrete, opaque, angular particles; and a slight and irregular undulation of the bands. Karpinsky (1906: 105, 151 et seq.) had already reached the conclusion that the radial striation of the lime-shell was due to recrystallization. On p. 105 he accurately described the dark bands in *Sycidium* as made up of minute, opaque particles, which he regarded as organic.

The small irregularities in the layering of the lime-shell, and the fact that the spacing of the bands does not gradually increase outwards, seem to exclude rhythmic precipitation after the type of Liesegang's rings (cf. Schade, 1928: 843).

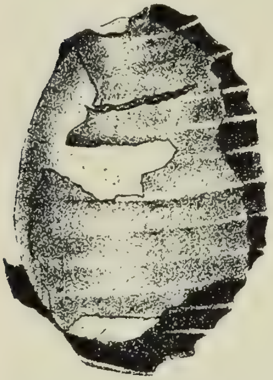
Although the banding of the lime-shell is seldom conspicuous in Recent or fossil gyrogonites, it is a significant structural character, especially well seen in the trochilisks. Similarity of structure betokens similarity of origin, and in this character also the trochilisks exhibit detailed agreement with the charophytes.

The lack of correspondence between the concentric layering and the ribbing or sculpture of the lime-shell in *T. podolicus* is still more marked in coronulate species of *Trochiliscus* if a U-shaped layering of their spiral cells be accepted. These examples seem to illustrate the commonly occurring 'independence of outer form and inner structure in an organic skeleton' (Sollas, 1921: 208). It has been shown that the tubercles of *Kosmogyra* are an integral part of the lime-shell (Reid & Groves, 1921: 185), and, according to Pia (1927: 90), they were developed late, the lime spirals being smooth at an earlier stage. In *Chara* (Karpinsky, 1906: fig. 40, p. 54; Reid & Groves, 1921: 182) and in *Sycidium* (Karpinsky, 1906: fig. 16) it is known that the final deposit of lime may considerably alter the appearance of the gyrogonite, and the various stages have been observed on the same specimen. The spirals, at first concave, may become flat, and finally convex; or, to use Peck's useful terminology, the first formed ridges are sharp and intercellular, later becoming rounded and cellular. According to Karpinsky (1906: 130, text-fig. 35, p. 50), the shape of the outer wall may be an important factor in determining the final form. Because of the variability of the sculpture within some species and even on the same specimen, this character has only a limited use in classification (for example, see Peck & Reker, 1948, on tubercles). In *Trochiliscus* a few of the coronulate forms figured by Peck have bipartite, or tripartite, ridges, which may be cellular or intercellular. In an important intermediate form, which is unfortunately not illustrated by a section, he found that two equal ridges represent each spiral cell, so that the number of ridges is twice the number of spiral cells. In *T. laticostatus* (Peck, 1934: pl. 11) the sculpture is exceptionally variable and it is difficult to feel convinced that all the forms are specifically related and differ from each other solely in the degree of calcification, especially as transitional stages do not seem to be developed on the same specimen.

Oospore membrane. The layered membrane forming the oospore wall has been studied in considerable detail in Recent charophytes, since its decoration, colour, and texture are characters of specific value (Allen, 1937). The tough outer layers, called the inner and outer coloured membranes by Groves & Bullock-Webster (1920: 56), are indurated and contain suberin (Nordstedt, 1889: 3; Overton, 1890: 36). The innermost layers directly investing the ovum are colourless and comparatively thin. The coloured and colourless layers are clearly shown by the Recent oospore in Text-fig. 6. In all species the outer coloured membrane is more or less strongly marked by spiral ridges or flanges derived from the lateral walls of the enveloping cells. In the Chareae the membrane is decorated with granules or tubercles. In the Nitelleae there are, in addition, reticulate types of decoration. The inner coloured membrane of all species is thinner and paler than the outer, and spiral ridges are not always shown; its decoration is always granulate, the granules being faintly, usually very faintly, indicated. The inner and outer membranes are often so closely adherent that they require a strong reagent to separate them (Groves & Bullock-Webster, 1920: 60).

There have been several records of the preservation of the oospore membrane in fossil charophytes. Reid & Groves (1921), for example, refer to well-preserved oospores in three species of *Gyrogonites* ('*Chara*') from the Eocene of Hampshire. But in no case has the decoration of the membrane been described and figured. Karpinsky (1906: 130) refers to the preservation of the membrane in *Lagynophora foliosa*. The photograph of *Lagynophora* sp. reproduced in Pl. 19, fig. 29, shows two fruits in approximately longitudinal section. The spiral ridges on the oospore membrane of the fruit on the left are cut tangentially. The oospore on the right, enlarged in Pl. 19, fig. 30, shows the somewhat contracted membrane in optical section; the transversely cut, broad-based ridges are clearly marked. This figure also provides definite evidence of a thin inner membrane. The figures of *Chara escheri* given in Pl. 19 show the excellent preservation of the original membranes in this Oligo-Miocene fossil; the detailed agreement with living *Chara* is pointed out below (p. 213).

The close comparison between the largely unaltered oospore membrane of *T. podolicus* and the membranes of Recent and fossil *Chara* is evident. Thus there is agreement in the brown, translucent character, and in the presence of a very similar granulate decoration. There is also some evidence of an inner and an outer layer. The way in which the fossil membrane has been cracked and disrupted in *T. podolicus* is closely paralleled in *Chara escheri*. The thickening of the edges of the minute pores through a few membranes of *T. podolicus* suggests a wound reaction. The only respect in which the oospore membrane of *T. podolicus* differs from those of Recent and fossil charophytes is in the absence of spiral ridges. Even in some Recent species, however, the ridges may be reduced to little more than faint lines (Groves & Bullock-Webster, 1920: 58).



TEXT-FIG. 6. *Chara fragilis*. Recent. Oospore with inner and outer coloured membranes partly scraped away exposing the intact colourless membranes. × *c.* 100. After Overton (1890). *Note*: The direction of the spiral ridges is reversed owing to the method of reproduction in the original.

Oospore contents. What is probably the true explanation of the origin of the vesicular contents of the oospore was suggested to me by Prof. T. M. Harris: that the vesicles represent starch-grains, the walls of the vesicles being the remains of the protoplasm and oil in which the starch-grains were embedded. The oospores of present-day charophytes contain oil and are tightly packed with rounded starch-grains. Some of these, showing the characteristic dark cross in polarized light, are represented in Text-fig. 1. Mirande (1919) stained the protoplasmic film surrounding the starch-grains with haematoxylin and found that 'les manteaux mitochondriaux, en contact serré, forment un pseudo-tissu cellulaire avec méats, d'où l'on peut, par une légère pression, faire sortir les grains d'amidon de leurs alvéoles'. His fig. 4 shows 'un fragment de ce pseudo-parenchyme mitochondrial dans lequel quelques grains d'amidon, contractés par déshydratation par l'alcool, se sont décollés des parois'. The same kind of structure is well illustrated in a section of the endosperm of maize (Sachs, 1882; fig. 50A), which shows polyhedral starch-grains surrounded by 'thin plates of dried-up fine-grained protoplasm'. The larger starch-grains of *C. hispida*, with a length of about 60 μ, are of the same order of size as the vesicles of *T. podolicus* (cf. Text-fig. 1). These observations support the explanation given above. Similarly vacuolated cell-contents found in fossil pteridophytes and cycadophytes have also been attributed to starch-grains (Seward, 1898: 212, fig. 41 A, B).

There appear to be no records of the remains of the contents of the oospore in other fossil Charophyta.

Summarizing these comparisons between *T. podolicus* and Recent and fossil charophytes, we find very close agreement in the size variation of the gyrogonite, and in the structure of the lime-shell and of the oospore membrane; there is probably agreement also in the nature of the oospore contents.

The general morphological resemblance between *T. podolicus* and living *Chara* is brought out in Text-fig. 1. In some respects the comparison, especially of the apical region, is closer with *Nitella* (see Text-fig. 5), though the fruits of this genus are not calcified.

In spite of the demonstration by Peck of the presence of coronulate cells in *Trochiliscus* spp., reservations have continued to be held about the charophyte nature of the trochilisks, especially *Sycidium* (Pia, 1937: 776). But in view of the additional structural evidence given above, and taking into consideration the evidence that the trochilisks were probably non-marine plants (p. 209), the charophyte affinity of *Trochiliscus* now seems to be established beyond all reasonable doubt. No attempt has been made by authors to answer the very convincing case put forward by Karpinsky that *Sycidium* should be regarded as a charophyte. The ill-founded comparison between *Sycidium* and marine codiaceous Algae, especially *Ovulites*, is not supported by the occurrence of *Sycidium*, along with *Trochiliscus*, in non-marine deposits.

VI. CLASSIFICATION OF *TROCHILISCUS*

Referring to Recent material, Groves & Bullock-Webster (1920: 86) have written: 'The Charophyta are extremely plastic, most species being subject to much variation of form . . .'; and on p. 88, 'aberrations from what is apparently the normal form of an organ in a particular species are common'. The charophyte gyrogonite has only a limited number of external characters by which species may be distinguished, and Groves (1933: 4) has referred to the hopeless task of trying to identify living species from 'imperfect detached fruits alone'. Harris (1939: 75 et seq.) has made a valuable survey of 'the relative magnitudes of the variation ranges of the individual species and of the family' (not including the trochilisks). He comes to the important conclusions that 'the range of the family does not appear great enough to allow a very large number of specific groups to be distinguished with any certainty'; and that 'the Charophyte gyrogonites are likely to be very difficult to determine specifically unless exceptionally abundant material is available, and even then difficult'. The inclusion of the trochilisks very considerably widens the range of form of the gyrogonite. In *Trochiliscus* the presence or absence of coronula cells, differences in the sculpturing, and in the number of spiral cells are additional characters for distinguishing species. Other characters may become available when the structure of more forms has been worked out.

When discussing the classification of the trochilisks Karpinsky (1906: 120) observed that the characters available for distinguishing species are generally variable and any classification based on them can claim to have no more than a provisional value. One of the characters to which he refers is the number of enveloping cells or ridges. Thus he included in *T. bulbiformis* forms with 8 or 10 as well as 9 ridges, and stated that *T. ingricus* 'usually' had 18 ridges. Similarly he recognized variation in the number of enveloping cells of *Sycidium* (p. 121). Peck (1934), on the other hand, while admitting some variation in *Sycidium* (p. 95), states his opinion that the number of spiral cells in *Trochiliscus* 'is a distinct morphological character . . . and a specific character of primary rank' (p. 102). Although the systematic value of this character has been considered at length by Karpinsky, it is necessary to return to the subject here because half the species of *Trochiliscus* recognized in America are distinguished by the number of enveloping cells alone and the same character is emphasized in a later paper dealing with structural trends in the Trochiliscaceae (Peck, 1936). The following observations provide further evidence in support of Karpinsky's view.

1. In each of three assemblages from different localities and horizons, Peck (1934: 103; 1936) found that the only constant difference between his species was the number of spiral cells or ridges. In the assemblage from the Mineola shale, which contained only non-coronulate forms, those with 10 ridges were common, while 9- and 11-ridged forms were comparatively rare, suggesting that the latter were variants of a 10-ridged species. Each of the other assemblages, those from the 'Sylamore' sandstone and the *Devonocidaris jacksoni* zonule, contained coronulate forms, which he divided into four species based on 8- and 9-celled specimens, which were abundant, and 7- and 10-celled specimens which were comparatively rare. In these two assemblages also it might be supposed that the rarer forms were variants of the commoner forms.

Peck (1934: 108) described *T. devonicus* (Wieland) from the Devonian of the Falls of Ohio as a non-coronulate form with 9 spiral ridges. '*Moellerina greenei*' Ulrich and '*Chara lemoni*' Knowlton also came from this locality, and they were stated in the original descriptions to have 'eight or nine strong angular, spiral ridges', and 'ten, or perhaps rarely nine, spirals (cells?)' respectively. The original figures and descriptions are more or less unsatisfactory, and the type material has not been traced. It is therefore of interest that five silicified specimens in the British Museum, labelled *Möllerina Greenei* Ulrich. Ohio Falls, U.S.A.,[1] should have 7, 8, 9, or 10 spiral ridges. The specimens agree generally in size, convolution, and shape with *T. devonicus*, and are alike except for the different numbers of spiral ridges. It appears therefore that the Falls of Ohio is a fourth locality in which this character shows an appreciable range.

2. Karpinsky (1906: 137) has emphasized the fact that the whorled parts of the plant which are homologous with the spiral cells are still very variable in Recent charophytes. Although the number of enveloping cells has been reduced to 5 in all genera since Palaeozoic times, naturally occurring variations in this number have been reported (Karpinsky, 1906: 136). Six spiral cells have been noted in a Recent and in a fossil fruit. Peck (1941: pl. 42, fig. 42) figures a 4-celled *Aclistochara* from the Cretaceous. In *Nitella*, 6, and in one case, 7, rudimentary enveloping cells have been seen in young 'oogonia'. Six, and 4, coronula cells have been found in *Chara*. Other teratological variations have been observed in abnormal fruits associated with normal reproductive organs. This abnormality takes the form of an additional whorl of enveloping cells, which show a tendency to twist in the same direction as the normal cells. The number of these enveloping cells is usually 5, but in *Chara foetida* there are sometimes only 4 (Goebel, 1918: 376), and in *C. contraria* var. *hispida* there may be 6 (Schmucker, 1927: 781). When both whorls are present, therefore, the total number of enveloping cells in Recent *Chara* may be 10 or, exceptionally, 9 or 11. It is very probable that such numerical variations, which are of no systematic value, were commoner in the earlier charophytes, as, for example, in *Sycidium*.

3. Numerical variation has of course been observed in many living plants, especially angiosperms, and the following example will serve to illustrate this. 'In the herb

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[1] These specimens were purchased at different times from Dr. F. Krantz, Bonn. Registered number V.13063.

Paris the flower is normally 4-merous, at least in *P. quadrifolia* and other species. But 5- and 6-merous flowers are exceedingly common as abnormalities, and this condition is the normal feature in *P. polyphylla*, in which even 7-merous flowers are not at all uncommon' (Worsdell, 1916: 60).

Very instructive parallels can also be found amongst fossil plants and animals. In the examples which follow there was not only considerable numerical variation (plasticity) in earlier species; but also, as in the Charophyta, a reduction in the number of parts in the course of geological time.

The first example is from the angiosperms. As a result of their study of the fruits of the London Clay and the Bembridge Beds, Reid & Chandler (1933: 42) found 'a considerable body of evidence pointing to reduction in the number of locules', and a greater variation in this number in earlier species. This is most clearly demonstrated by *Sparganium*. *S. multiloculare* from the Oligocene had 5-4-3-2-loculed forms; *S. ovale* from the Mio-Pliocene had 2- and 1-loculed forms; forms of *S. ramosum* from Interglacial beds had 4, 3, or 2 locules; and the living genus is usually 1-loculed, but two species are 2-loculed, and *S. ramosum* may rarely have two locules. 'The chain of evidence is rather interrupted and irregular, but undoubtedly points to a reduction in the number of locules having occurred.'

The other example is from the animal kingdom. With few exceptions the major part of the test in the Mesozoic and later echinoids is formed of 20 columns of calcite plates; but in the Palaeozoic echinoids the number of columns is variable and often great (Woods, 1947: 136). *Melonechinus multiporus* is an example of a Lower Carboniferous species in which the number of columns varies from 85 to 95 (Jackson, 1912: 375). Numerical deviation from regular penta-symmetry has been observed in many fossil and some Recent species of the Crinoidea (Bateson, 1894: 435). Bather (1889: 166) put forward the view that the Echinodermata were at first less definite in their plan of structure, but that through variation and natural selection the pentamerous type has become fixed. Much the same thing seems to have happened in the Charophyta.

4. Harris (1939) has shown that the size ranges of the Purbeck charophytes varied within a species by about ±20 per cent. of a mean. The gyrogonites of three species of *Clavator* were found to have a total range in length of 240–660 μ. This may be compared with ranges of only 300–400 μ, 700–1,000 μ, and 600–800 μ given by Peck for the assemblages of *Trochiliscus* considered in the first section above. The range in each of these assemblages is less, not more, than the range in *T. podolicus*, which shows the normal variation. It must therefore be concluded either that size variation is of no value in delimiting closely allied species of *Trochiliscus*, or that fewer species are present than has been supposed.

For these reasons it is considered better not to regard the number of enveloping cells in each species of *Trochiliscus* as constant, but rather to recognize that there may be variations in this as in other characters of the gyrogonite. Although the number of spiral cells appears to be fixed in some species, in others there is evidence of a rather wide variation, e.g. from 7 to 10, or 9 to 11. The taxonomic changes required if such variation within a species be accepted are summarized below (p. 209).

The difficult question of the classificatory value of the sculpturing of the gyrogonite is touched on above, p. 202.

Regarding another character of the *Trochiliscus* gyrogonite, Peck (1934: 103) writes: 'Although the calcification of the coronula cells may be considered of greater than specific value, I have regarded it as a further trend towards calcification that might well be developed independently among species of different genera.' The calcification of the coronula cells is found in no other charophyte genus, *Aclistochara* excepted. It is therefore highly distinctive of those species of *Trochiliscus* in which it occurs. It is natural to assume that the apparently non-coronulate species of *Trochiliscus* had coronula cells which have not been preserved. If they were truly non-coronulate, the division between the coronulate and the non-coronulate species-groups would undoubtedly merit the establishment of a new genus for the former. But there does in any case seem to be a rather clear distinction between them: for the coronulate species have a large-celled coronula and a funnel-shaped opening; whereas the remaining species, when complete, usually have a beak with a small apical opening, which presumably supported a small coronula.[1] Peck (1934: 92) states that there is 'little possibility for mistaking these "non-coronulate" forms for "coronulate" specimens that have lost the coronula cells'. The distinction may be likened to that found in Recent charophytes: the coronula is well developed and persistent in *Chara*, and is inconspicuous and often deciduous in *Nitella* (Groves & Bullock-Webster, (1920: 53)). A further distinction between the two groups is that the spiral ridges of non-coronulate forms are simple and sharp and do not show the varied sculpturing of the coronulate species. The coronulate forms also show less range in size than the non-coronulate and are generally larger. It may also be significant that the known time ranges of the two groups are somewhat different: the non-coronulate forms are found in rocks of early Lower Devonian to Upper Devonian age; the coronulate forms in rocks of late Lower Devonian to basal Mississippian age. To give taxonomic expression to these differences it is proposed to group the coronulate forms in a new sub-genus which may appropriately be named *Karpinskya*, after the author who laid the foundation for all subsequent work on the trochilisks. The remaining, non-coronulate, forms are grouped under the sub-generic name *Eutrochiliscus*.

CHAROPHYTA

Family TROCHILISCACEAE

Genus ***TROCHILISCUS*** Karpinsky 1906

Gyrogonites spheroidal or bulbiform, about 300–1,000 μ in diameter. Lime-shell externally (and sometimes internally) sculptured with continuous ridges or furrows representing about 7–18 dextrally spiralled enveloping cells, which originate around a cylindrical basal opening and extend to the summit; layered structure probably more or less concentric and evenly spaced. Apical opening expanded medially or funnel-shaped. Coronula cells, when preserved, equal the enveloping cells in number and form a ring round the apical opening. Oospore filled with starch-grains (?). Oospore membrane resistant, originally suberised (?), decorated, probably two-layered.

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[1] In diagnoses of three non-coronulate forms—*T. devonicus*, *T. bellatulus*, and *T. rugulatus*—it is stated that 'a low ridge connects the apical ends of the spirals' (Peck, 1934). It seems from a comparison with the Mineola shale specimens, and other species, that this description should be applied to the basal, not the apical, ends.

Sub-genus EUTROCHILISCUS nov.

DIAGNOSIS. Species of *Trochiliscus*, generally of small size. Coronula cells not known, probably small. Spiral ridges probably intercellular and equalling the enveloping cells in number.

SPECIES. *T. ingricus* Karp., type species; *T. bulbiformis* Karp.; *T. devonicus* (Wieland) Peck (*T. rugulatus* Peck); *T. convolutus* Peck (*T. minutus* Peck, *T. multivolvis* Peck); *T. podolicus* Croft.

DOUBTFUL SPECIES. *T.* (*Moellerina*) *greenei* (Ulrich); *T. lemoni* (Knowlton); *T. bellatulus* Peck.

DISTRIBUTION. Eastern Europe: Lower Devonian (Downtonian) to Middle Devonian. North America: late Lower (?) Devonian to Upper Devonian.

Sub-genus KARPINSKYA nov.

DIAGNOSIS. Species of *Trochiliscus*, of medium and large size. Coronula cells large, calcified. Spiral ridges often multiple and then 2–4 times as numerous as the enveloping cells.

SPECIES. *T. laticostatus* Peck (*T. septemcostatus* Peck, *T. octocostatus* Peck, *T. decacostatus* Peck), type species; *T. bilineatus* Peck (*T. meeki* Peck, *T. liratus* Peck, *T. raricostatus* Peck); *T. herbertae* Peck.

DISTRIBUTION. North America: late Lower Devonian to basal Mississippian.

VII. HABITAT OF THE TROCHILISKS

Recent charophytes live mainly in fresh water, though some species prefer brackish conditions; none can tolerate a normal marine environment. In the past also, charophyte remains are found typically in deposits laid down in fresh water, for example, the Purbeck lake beds.

Karpinsky (1906: 140) showed that in Russia trochilisks were very seldom associated with marine organisms, and concluded that the sandy and muddy strata in which they normally occurred were littoral, shallow-water, deposits. He further pointed out that the associated marine fossils in the American occurrences were not deep-sea but off-shore forms.

On this subject Pia (1937: 777) has written: 'Alle Forscher scheinen bisher der Ansicht gewesen zu sein, daß die Trochilisken und Syzidien meerische Versteinerungen sind (vergl. bes. PECK, 1934, S. 93 und 102). Um so überraschender ist es, daß HECKER, der beste Kenner des russischen Devons, sie jetzt (1935 *b*, S. 57–58) unter den Formen der Binnenbecken anführt, die in brackischen bis süßen, vielleicht aber stellenweise auch in übersalzenen Wässern lebten.'

More recently, Hecker (1941: 77, 81) points out that fishes and trochilisks frequently occur together to the exclusion of all marine invertebrates. He considers that the Middle Devonian beds in which *Trochiliscus* and fishes occur were laid down in 'running water' (Pärnu beds), and in a 'dying bitter salt lagoon gradually filled with delta sands and barkhans' (Narova beds). Of the Upper Variegated Series (Upper Devonian) he writes (p. 81): 'The marls enclose a multitude of trochilisks and most probably represent lake deposits.' In Podolia, as in Russia, *Trochiliscus* is associated with fishes and ostracods, and definite marine fossils are lacking. The Czortkov series consists of passage beds in which some marine horizons occur. The overlying beds of the Podolian Old Red contrast markedly with the contemporaneous marine beds of the region, and were almost certainly continental (mainly fluviatile) in origin (see Zych, 1927: 48; Samsonowicz, 1950: 504).

In the light of this evidence that the European trochilisks were probably aquatic land-plants, it is interesting to reconsider the American occurrences. It is true that *Trochiliscus* occurs, sometimes abundantly, in purely marine limestones, for example the Jeffersonville and Columbus limestones, along with a large marine shelly fauna of littoral type. It is, however, significant, and requires further investigation, that the beds from which Peck obtained much of his material, i.e. the Bushberg sandstone, the Grassy Greek shale, and the shale below the Mineola limestone, are all basal deposits, less than 30 m. thick, laid down in advancing and transgressive seas (Branson, 1922; 1944). The Bell shale, which forms 'a pocket in the Dundee limestone' (Peck, 1934: 116), and the Cerro Gordo substage of the Hackberry stage (Fenton, 1919: 358), are further examples. In such conditions it is possible that the mantle of a flooded land area has contributed to the deposits, and very probable that some of the sediments were laid down in brackish estuaries or lagoons. Indeed, in the Bushberg sandstone, Bell shale, and Grassy Creek shale, a marine shelly fauna is sparse or absent. Grabau, quoted by Branson (1922: 8), writes that the Noel shales (which are very similar to, and probably the lateral equivalents of, the Grassy Creek shale) 'can only represent the reworked residual soil of an old peneplain surface which was slowly submerged beneath the advancing Mississippian sea'.

The mode of occurrence of *Sycidium* in the Devonian of south-western China (Lu, 1948) is also very instructive.[1] The beds assigned to the Lower, Middle, and Upper Devonian of P'oshi in eastern Yunnan have a total thickness of about 1,660 m. Except for a few hundred metres of unfossiliferous sandstones at the base, the formation consists of a series of limestones, most of which contain a shallow-water marine shelly fauna, together with sandstone and shale horizons in which poorly preserved remains of vascular land-plants occur. The plants have been described by Hsü (1947), who assigns them to *Protolepidodendron*, cf. *Drepanophycus*, and other Devonian genera (see also Halle, 1936). In the highest and lowest plant-bearing horizons, marine shells are associated with the plants. No marine fossils, with the possible exception of the ostracods, are found in the series of beds which includes the limestone containing the abundant material of *Sycidium* described. This limestone is immediately overlain by a thick sandstone horizon with land-plants, *Lingula*, and fish-remains. It is underlain by limestones with abundant ostracods at the base. Below these occurs the main plant horizon, consisting of 70 m. of sandstone with layers of shale. *Sycidium* is also found at a second, higher, horizon where it is associated with abundant corals in a succession of marine limestones. Hence the Chinese *Sycidium*, which is identified with the largest and commonest Russian species, *S. melo* Sandb., occurs in both marine, and non-marine or brackish, deposits. At the upper horizon the fruits may have been washed into a marine environment. At the lower horizon they may, like the nearly associated vascular plants, have been derived from the land, or have grown in brackish lagoons from which a marine fauna was excluded.

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[1] I am much indebted to Dr. J. Hsü, Curator of the Birbal Sahni Institute of Palaebotany, for providing me with a copy of this paper.

In this, as in many similar discussions on the environment of fossil groups, due weight must be given to the fact that while land-living organisms are frequently washed into the sea, marine organisms very rarely get preserved in continental deposits. It is therefore easier to explain the occurrence of fresh- or brackish-water trochilisks, even in abundance, in marine limestones than it is to explain the occurrence of marine trochilisks in equal abundance in lake or river deposits. Meek (1873: 219) wrote long ago that if the minute bodies in the Columbus limestone of Ohio were the fruits of the freshwater genus *Chara*, 'they must have been carried into the sea by streams, and deposited where we now find them, along with numerous marine shells'. The suggestion that tangles of charophytes may have drifted out to sea has been made by Groves (1933: 6). Cf. Pia (1931: 17).

It may be concluded therefore that the evidence from the American and Chinese occurrences of *Trochiliscus* and *Sycidium* generally supports that from Europe. At most horizons and localities in Europe, Asia, and America it is probable that the trochilisks had a fresh- or brackish-water, rather than a marine, habitat. At other horizons it may be assumed that the fruits were transported from the land into a shallow water, marine environment.

The preservation of the fruits of *T. podolicus* also gives a clue to their habitat. The infiltrated calcite in which the oospore membrane and contents are preserved may have been formed in the same way as in some Recent *Chara* marls, that is, by the redeposition of calcium carbonate dissolved by water percolating through the marl (Davis, 1901: 496); for it is probable from the worn nature of some of the specimens, and from the absence of vegetative axes, that the gyrogonites were derived from a contemporaneous deposit.

Supplementing the geological evidence on the habitat of the trochilisks is the biological evidence furnished by the fossils themselves. Among the freshwater Green Algae the membrane secreted round the egg after fertilization usually undergoes considerable thickening and constitutes a resting-spore in which abundant food reserves are stored. Such spores, of which the charophyte oospore is an example, are able to withstand prolonged desiccation and may retain their vitality over long periods. In the vast majority of marine Algae, on the other hand, there is no resting period and the zygote grows at once into another organism (Fritsch, 1935: 49, 50). The possession of a resting-spore with a 'lignified' or 'cutinized' coat was regarded by Church (1919: 30–32) as the most obvious criterion of those plants which had become partially or wholly adapted to life on land. Hence the demonstration that

Trochiliscus had large spores with a resistant (? suberised) wall, further protected by a thick lime-shell, and the evidence of food reserves in the form of starch, strongly suggest, when taken together, that the fossils were resting-spores of a plant which had already become adapted in some degree to a non-marine habitat.

VIII. THE MORPHOLOGY OF *CHARA ESCHERI* UNGER

(PL. 19, FIGS. 21–27; TEXT-FIG. 7 A, C)

The following account of the well-preserved gyrogonites of this Tertiary species is the first illustrated description of the detailed structure of the oospore membrane of any fossil charophyte, other than *T. podolicus*. It brings out the fundamental agreement between the fruits of fossil and living *Chara* and at the same time strengthens the relationship between this genus and the Devonian *Trochiliscus*.

A synonymy of *Chara escheri* is given by Groves (1933: 17). This species was first clearly described and figured by Heer (1855) from Swiss material of Oligocene-Miocene age. The clearest figures are given by Unger (1860: pl. iv, figs. 1–5). Gaudin (1856) gave a detailed, but unillustrated, account of the morphology and confirmed Heer's observation that the lime-shell, when broken away, revealed the coal-black organic membrane surrounding the spore. The latter was filled with white calcite replacing the ovum. The microscopical characters of the spore membrane were not described. The homology of the lime-shell and the oospore membrane with the corresponding parts in Recent *Chara* was clearly recognized.

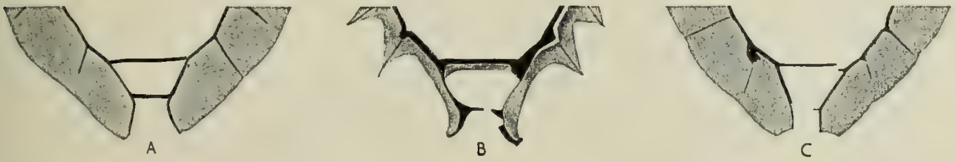
The material available for the present study is a piece of dark grey shale, registered number V.17236, containing numerous brown fruits which can be dug out with a needle. The specimen is labelled '*Chara Escheri* A. Br. Miocene. Rochette. Switzerland. Presented by Dr. Ph. De la Harpe.' It was in material from this locality that Heer (1855: 26) noted the presence of a black oospore membrane. According to Heim (1919: 130, 140) the Molasse at Rochette is of Upper Oligocene and Lower Miocene age.

The gyrogonites were treated in the manner described above for *Trochiliscus* (p. 192): about 50 were embedded together in one plane and sectioned; a small number were dissolved in hydrochloric and hydrofluoric acids, and the demineralized membranes were then mounted in gum chloral. Some of the gyrogonites are filled with pyrite in place of calcite, and patches of pyrite are often present in the somewhat recrystallized lime-shell. On decalcification the lime-shell maintains its shape and appearance. Between the lime-shell and the oospore membrane there is sometimes a thin layer of secondary silica.

Longitudinal sections (Pl. 19, figs. 21–23) show the structure clearly. The oospore membrane is plainly recognizable within the robust lime-shell; and the thickened lateral walls of the enveloping cells, which stand out as wide spiral flanges when the gyrogonites are demineralized, are well developed. At the base of the oospore the walls of the turning cell and the node-cell are thickened to form a well-marked cage, preserved in the same way as the oospore membrane. In one or two specimens there is a transverse partition across the cage (Pl. 19, fig. 23; text-fig. 7 A, C).

In only one of the sectioned specimens is the layering of the lime-shell clearly shown. The dark bands, which are rather evenly spaced at about 3 μ, are more or less concentric with the oospore (Pl. 19, fig. 28).

The oospore membrane is double and about 5 μ thick. It is usually much cracked and disrupted. A few of the membranes from demineralized gyrogonites are perforated with irregularly spaced, rounded holes (Pl. 19, fig. 25) which have no doubt been bored by some organism. The outer membrane is dark brown and translucent with a semi-tuberculate decoration, the rounded granules being non-contiguous and of variable size (Pl. 19, fig. 24). The thin inner membrane is seen on torn edges and on the edges of the holes. It is pale brown by transmitted light and has a rather indefinite, granulate decoration (Pl. 19, fig. 26). The inner membrane is also seen in a few of the sections as a thin contracted brown line (Pl. 19, fig. 21). The spiral ridges on the membrane, marking the position of the lateral walls of the enveloping cells, are clearly shown (Pl. 19, fig. 24). The lateral walls, or flanges, are decorated with irregular granules which are coarser than those on the inner and outer membranes (Pl. 19, fig. 27). Remains of the organic contents of the oospore are not preserved.



TEXT-FIG. 7. The cage at the base of the oospore in longitudinal section. A, C. *Chara escheri*. Oligo-Miocene. V.28559. B. *Chara hispida*. Recent. V.28356. All × *c*. 75. (N.B. See Addendum, p. 216.)

It will be clear from a comparison with Text-fig. 1 B that there is a striking agreement between the structure of *C. escheri* and Recent *Chara*. The presence of a cage is especially interesting. The cages of the two species are compared in Text-fig. 7 (see also Text-fig. 1 B and Pl. 19, fig. 23). The statement by Groves & Bullock-Webster (1920: 58) that the cage at the base of the oospore encloses the stalk-cell appears to be inexact; for the 'transverse growth' to which they refer no doubt represents the thickened wall between the turning cell and the node-cell, or between the node-cell and the stalk-cell. Presumably it is the wall between the turning cell and node-cell, but there appears to be no statement on this in the literature (cf. de Bary, 1875: 300).

The layering of the lime-shell is discussed on p. 201 above.

The oospore membrane agrees in all respects with the equivalent membrane of existing charophytes. The inner and outer layers correspond to the inner and outer coloured membranes (Text-fig. 6) of Groves & Bullock-Webster (1920: 56). Pl. 19, fig. 24 of *C. escheri* may be compared with the decorated outer membrane of *C. vulgaris* in Pl. 19, fig. 20, and with the figures in Groves & Bullock-Webster. And the decorated inner membrane of *C. escheri* may be compared with the corresponding membrane of *Nitella* figured by the same authors (1920: pl. v, fig. 5). The decorated flange in Pl. 19, fig. 27 much resembles the flange of *Nitella* in their pl. iv, fig. 8.

The work on the Purbeck Charophyta has fully justified Pia's (1927) action in transferring *Chara*-like fossil fruits with five smooth lime spirals to a provisional genus, for which he has revived the name *Gyrogonites* Lamarck. This has been criticized by Peck (1941: 288) and by Rásky (1945: 29), who prefer to retain the name *Chara*. It is, however, clearly undesirable that a form-genus used for fossil material should bear the same name as a well-defined living genus; and there seems to be little risk of confusion between *Gyrogonites* as a generic name and 'gyrogonite' as a descriptive term, even when both words are capitalized. Harris (1939: 73, 74) finds that several of the fossil fruits formerly described as *Chara* cannot be distinguished with certainty from Purbeck species. It does not, however, seem possible to include *C. escheri* in *Perimneste horrida*, because the apex of the latter is uncalcified. Although it is not improbable that one or more extinct genera had an internal structure essentially like that of Recent *Chara*, the very close morphological agreement between the Tertiary form *C. escheri* and existing *Chara*, especially the presence of a cage at the base of the oospore, seems to justify the inclusion of this species in the living genus. According to Groves & Bullock-Webster (1920: 58) a cage is not developed in the Nitelleae. Wide spiral flanges are, however, more characteristic of *Nitella* than of *Chara*, but the fossil fruits are not laterally flattened as in that genus.

IX. SUMMARY AND CONCLUSION

1. The genus *Trochiliscus* was founded on charophyte fruits (gyrogonites) from the Middle Devonian of north-west Russia and Esthonia—the only previous record from the Old World. It later proved to be well represented in Middle and Upper Devonian, and basal Mississippian beds in North America. The species described here, *T.* (*Eutrochiliscus*) *podolicus* n.sp., is from a new area, west Podolia, on the borders of Poland and Russia. It is of Lower Devonian (Downtonian) age and is the earliest charophyte of which there is reliable evidence.

2. The calcified gyrogonites are unusually well preserved and permit detailed comparisons to be made with living and extinct charophytes. General agreement is found with the fruits of *Chara hispida*, of which longitudinal sections have been prepared. In the shape of the apical opening of the lime-shell the comparison is closer with the uncalcified envelope of *Nitella* fruits. The layered structure of the lime-shell is very similar to that of living and fossil *Chara*, and also to that of *Sycidium*. The resistant, decorated, oospore membrane differs little from the corresponding membrane of living Charophyta and of the Tertiary species *Chara escheri*. A vesicular mass often present within the oospore membrane appears to represent the contracted starch-rich contents of the oospore. These new observations on the structure of the gyrogonites, and the demonstration that their size variations are almost the same as in *Chara vulgaris*, amply confirm the charophyte relationship of *Trochiliscus*.

3. The classification of *Trochiliscus* is discussed. Karpinsky's view that the number of spiral enveloping cells may vary within a species is upheld. Adoption of this view leads to a reduction of the number of species from about 17 to 8. The species are placed in two new sub-genera, *Eutrochiliscus* and *Karpinskya*, distinguished mainly by the presence or absence of large calcified coronula cells. The time range of *Eutrochiliscus* is from Lower Devonian (Downtonian) to Upper Devonian; and of *Karpinskya* from late Lower Devonian to basal Mississippian.

4. The trochilisks were considered by Karpinsky and by Peck to be marine plants. Recent stratigraphical work indicates, however, that the deposits in which the Russian trochilisks were entombed were continental, and hence that the plants probably lived in fresh or brackish water. The Podolian occurrence supports this view. Much of the North American material comes from basal deposits to which residual soils of invaded land-masses probably made a large contribution. In China, *Sycidium* occurs in abundance in a limestone between two sandstone horizons in which vascular land-plants, but no marine organisms, are found. The comparatively rare occurrences of trochilisks in littoral marine environments are probably to be explained by drifting. The resistant membrane round the oospore, which may have contained food reserves in the form of starch, indicates that the plants were adapted, like living freshwater Algae, to periods of desiccation. The conclusion is reached that the trochilisks were probably fresh- or brackish-water plants. This accords with the known habitats of living and fossil charophytes, and removes one of the reasons advanced against their Characeous affinity. In this connexion it is interesting to recall the contemporaneous occurrence of *Palaeonitella* in the Rhynie peat-bed.

The trochilisks seem to be rather typical of thin basal deposits laid down at breaks in the stratigraphical succession. For, in addition to several North American examples, the beds in the Leningrad area in which trochilisks are particularly abundant were laid down immediately above a major unconformity. In the absence of marine fossils, trochilisks are suggestive of fresh- or brackish-water conditions of deposition.

5. Important details of the structure of a Tertiary charophyte fruit, the Oligo-Miocene species *Chara escheri*, are described and figured for the first time; several points of agreement with *T. podolicus* are shown. The layered lime-shell, decorated oospore membranes, and cage at the base of the oospore agree closely with the corresponding structures in living *Chara* and justify the inclusion of the fossil species in the same genus.

6. We know through the work of Peck that there is a hiatus within the Carboniferous period between the ancient trochilisks on the one hand and the fruits of modern aspect with five spiral cells on the other; the two groups do not overlap in time, and, with the exception of *Palaeochara*, there are no intermediate forms. It is to be hoped that further collecting will bridge this gap. Despite these differences, the distinctive features of the fruits of both groups—the large oospore with a resistant membrane surrounded by enveloping cells in which lime is deposited to form a layered shell—have persisted essentially unchanged from a period not later than the early Devonian. The main trends have been towards a reduction in the number of enveloping cells, a loss of plasticity, and a change in the direction of coiling. In the early types the number of cells was less definite, often 8, 9, or 10, and up to 18, but the present number (5) had already become stabilized before the close of the Carboniferous period. By the same time, forms with straight enveloping cells (which were probably the most primitive), and dextrally coiled forms, had been completely replaced by forms with sinistral coiling. Comparable examples of reduction, with loss of plasticity, are noted in the fossil history of the echinoderms and of certain angiosperms. Judging from *T. podolicus*, the oospore membrane of *Trochiliscus* was very thin ($1\,\mu$), while

the equivalent figures for *Chara escheri* and *Chara hispida* are 5 μ and 10 μ, respectively. These figures appear to indicate a trend towards increased protection of the zygote against desiccation. The fact that the lime-shells of living charophytes are generally thinner than those of fossil forms may perhaps be correlated with it.

The Charophyta, which are related cytologically to the haplobiontic seaweeds, especially the Chlorophyceae, are of unusual interest in regard to the adaptation of marine Algae to subaerial conditions. Church (1919), in a detailed study of this question, referred to *Chara* as 'the transmigrant failure'. Bower (1935: 489) has attributed the 'stolid conservatism' of the charophytes to the fact that they did not 'hit on the innovation of postponing meiosis by interpolation of a diploid phase'. The trochilisks not only widen our conception of the Charophyta, and demonstrate that the fruits of the early charophytes were basically like those of today, but show that their earliest representatives were already adapted to a land habitat in very ancient times. The fact that the remains of trochilisks have not been found along with marine calcareous Algae in the extensively searched littoral deposits of Lower Palaeozoic age may be due to inadequate collecting. If this is not so, it suggests either that the development and calcification of their highly specialized fruits were delayed until they began to adopt a land habit; or that they had already emerged from the sea and become established on the land some time before the beginning of the Devonian period.

Pia (1940: 154; 1942: 12) has stressed the remarkable fact that the Devonian trochilisks came into prominence and reached their peak at a time when other calcareous Algae had greatly declined. Although it is difficult to account for the impoverishment of the marine calcareous floras, the local abundance of the Charophyta may be explained by evolutionary changes leading to the adoption of a new and more favourable environment in which there was probably little competition from other plants.

The much-debated affinity of the Charophyta is in no way elucidated by a study of their earliest representatives: they seem to have been just as isolated in the Devonian as they are today. The Charophyta stand out as a group that became highly specialized and adapted to life on land at a very early period, and has subsequently proved to be not only extremely conservative, but also remarkably persistent.

ADDENDUM

The interesting account by Maslov (1947) of the structure of '*Chara*' *meriani* from Russian Tertiary deposits was not seen until this paper was in the press. The gyrogonites were studied in thin longitudinal sections, which demonstrated the two-layered character of the lime-shell, as well as other features. The inner layer has slightly concave or convex, concentric laminations, and it is clear from his drawings and descriptions that the banding of the calcite compares closely with that of other charophytes, for example, *C. escheri* (Pl. 19, fig. 28). The outer layer, however, which was evidently deposited on the outer wall of the spiral cells, is composed of clear, yellowish calcite, and does not show laminations. In a small number of specimens the inner and outer layers are separated by flattened tubular spaces representing the lumens of the spiral cells, and these spaces form a line of weakness along which the outer layer sometimes splits off. Deposition of lime in this way on both the inner and the outer walls of the spiral cells is not known in any Recent charophyte, nor in *C. escheri*, but it is a well-established feature of the Clavatoraceae (Harris, 1939: 36, text-fig. 71), and may have a wider significance.

Maslov also demonstrated that in his material the upper part of the basal opening of the gyrogonite is closed by a calcareous plate, a feature which had not previously been noted in the Charophyta. This basal plate, which is laid down on the inner wall of the turning cell, is also present in the living *Chara hispida* and is shown in Text-figs. 1 B and 7 B. A calcareous plate or plug of varied development also occurs in the basal opening of *C. escheri* and is erroneously omitted from Text-figs. 7 A, C. In this fossil species the upper surface of the plate, which is in contact with the base of the oospore membrane, is flat, or slightly concave or convex. The lower surface is usually more or less strongly concave and may be asymmetrical. In one or two specimens the plate is so thick that it fills the upper part of the basal opening, and in the specimen in Pl. 19, fig. 23 (but not shown in Text-fig. 7 A) its lower surface is in contact with the transverse septum.

It is clear that much has still to be learnt about the structure of the charophyte lime-shell, and it is very desirable that many more species, both fossil and Recent, should be examined in thin section.

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All the figures are from untouched photographs. The specimens in Figs. 1–5 were lightly coated with ammonium chloride. The photographs for Figs. 1–5, 15, 21–23, 29, and 30 were taken with Leitz Ultropak equipment. All the specimens figured, except Fig. 20, are in the Department of Geology, British Museum (Nat. Hist.). The transmitted light photographs were taken by Mr. H. M. Malies.

PLATE 18

Trochiliscus podolicus n.sp., L. Devonian. Figs. 1–16. Pages 194–199.

FIGS. 1, 2. Lateral and basal views of the holotype with 10 dextrally spiralled ridges springing from a small basal opening; 11–12 ridges are seen in lateral view. × 58. (V.28340.)

FIGS. 3–5. Three gyrogonites in lateral view. The spiral ridges bend upwards on to the prominent beaks of two of the specimens. All × 58. (V.28338; V.28341; V.28339, respectively.)

FIG. 6. Median longitudinal section of a specimen freed from the rock. The basal and apical openings are clearly defined by dark infillings of matrix and reddish mineral. The central cavity of the lime-shell is filled with clear calcite. × 60. (V.28348.) Cf. Text-fig. 2E.

FIG. 7. Another specimen from the same slide showing the ridged lime-shell with apical and basal openings. The calcite of the central cavity extends into the narrow part of the apical opening, the expanded portion being filled with matrix. The contracted oospore membrane forms a ring enclosing traces of the organic remains of the ovum. × 60. (V.28348.) Cf. Text-fig. 2A.

FIG. 8. Equatorial section of a specimen in the rock showing the circular outline of the dark structureless lime-shell. The contracted oospore membrane is double as though an inner and an outer layer had separated. × 60. (V.28349.)

FIG. 9. Transverse section of specimen in the rock. The incomplete lime-shell shows regular layering throughout. × 60. (V.28352.)

FIG. 10. Part of Fig. 9 at a higher magnification showing the regular layering more clearly. × 180. (V.28352.)

FIG. 11. Another example of the regularly spaced, slightly undulating, layering of the lime-shell in a section of the rock. × 180. (V.28349.)

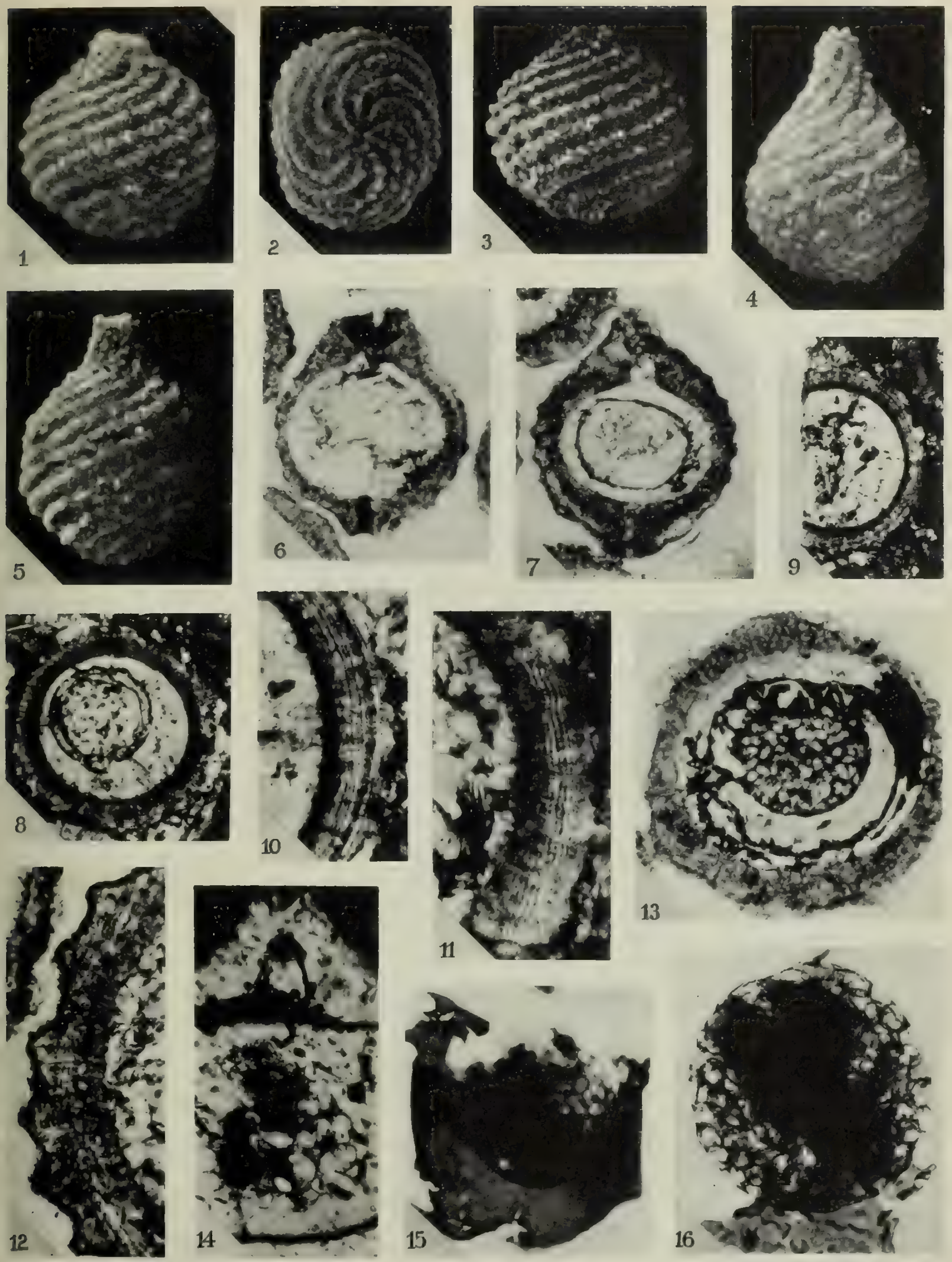
FIG. 12. Portion of the thick lime-shell of a specimen freed from the rock showing the ridges and rounded furrows in cross-section. The layering, faintly seen, appears to be more or less concentric and unrelated to the sculpturing. × 180. (V.28348.)

FIG. 13. Transverse section of a gyrogonite freed from the rock showing the ill-defined lime-shell, the disrupted oospore membrane, and the contracted vesicular contents with rounded outline. × 100. (V.28348.)

FIG. 14. Middle portion of a median longitudinal section through a gyrogonite. A few distinct rounded vesicles represent part of the oospore contents. A peak-shaped membrane attached to the oospore membrane projects towards the apical opening. × 180. (V.28348.)

FIG. 15. Globular vesicular body, still partly enclosed in the oospore membrane, dissolved out of a gyrogonite. × 94. (V.28347.)

FIG. 16. The contracted contents of a similarly treated specimen showing the vesicular structure clearly, at a higher magnification. × 180. (V.28346.)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TROCHILISCUS

PLATE 19

Trochiliscus podolicus n.sp., L. Devonian. Figs. 17–19. Page 197.

Fig. 17. Portion of an oospore membrane, dissolved out of a gyrogonite, with a decoration of small irregular granules. × 500. (V.28346.)
Fig. 18. Portion of the oospore membrane of another specimen with a similar, but unusually coarse, decoration. × 500. (V.28345.)
Fig. 19. Oospore membrane, dissolved out of a gyrogonite, with more or less circular thickenings, some of which have a minute central pore. × 500. (V.28556.)

Chara vulgaris L. Recent. Fig. 20. Page 213.

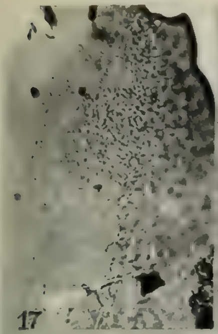
Fig. 20. Portion of an oospore membrane, for comparison with Figs. 17, 18, 24. The decoration is semi-reticulate, the rounded granules being non-contiguous and of variable size. The dark parallel lines are short lengths of the spiral ridges. × 500. (G. O. Allen Colln.)

Chara escheri Unger. Oligo-Miocene. Figs. 21–28. Page 212.

Fig. 21. The upper portion of a longitudinal section through a gyrogonite showing the outer oospore membrane and the thin inner membrane, which has contracted away from it. × 58. (V.28559.)
Fig. 22. Gyrogonite in longitudinal section. The thick lime-shell, basal opening, and black oospore membrane with prominent flanges between the lime spirals are clearly shown. × 58. (V.28559.)
Fig. 23. The lower portion of a gyrogonite in longitudinal section. The basal opening of the lime-shell is lined by a membrane forming a cage at the base of the oospore; the cage is divided by a transverse wall (cf. Text-fig. 7A). Portions of other gyrogonites show the well-developed flanges on the oospore membrane. × 86. (V.28559.)
Fig. 24. Oospore membrane with a semi-tuberculate decoration, the rounded granules being non-contiguous and of variable size. The spiral ridges to which the flanges are attached are strongly marked. × 485. (V.28560.)
Fig. 25. Portion of oospore membrane with three sub-circular borings. The inner, more translucent, membrane is seen on the edges of the holes. × 230. (V.28560.)
Fig. 26. Portion of a similarly bored membrane. The dark outer membrane has largely been removed exposing the thin inner membrane, which has a rather indefinite granulate decoration. × 485. (V.28560.)
Fig. 27. Portion of the spiral flange of an oospore with a well-marked decoration of irregular granules. × 485. (V.28560.)
Fig. 28. Portion of the wall of a gyrogonite in longitudinal section showing the fine banding of the thick lime-shell and the convex profile of the lime spirals. The black disrupted oospore membrane is seen on the left. × 175. (V.28559.)

Lagynophora sp. Eocene (Liburnian). Figs. 29, 30. Page 203.

Fig. 29. Approximately longitudinal section through a fertile node exposed on a polished surface of the rock. In the fruit on the left the spiral ridges of the oospore are cut tangentially; in the fruit on the right they are cut transversely. × 36. Monte Spaccato, Trieste. (V.17155.)
Fig. 30. Portion of the oospore on the right of Fig. 29, enlarged. The strong spiral ridges on the oospore membrane are seen in transverse section; in places the thin inner membrane has become separated from the outer membrane. × 94. (V.17155.)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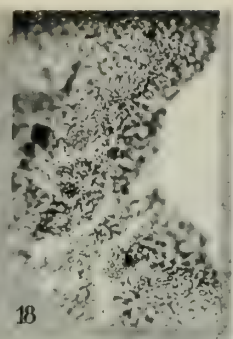
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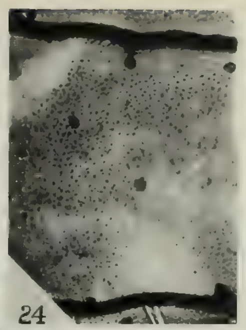
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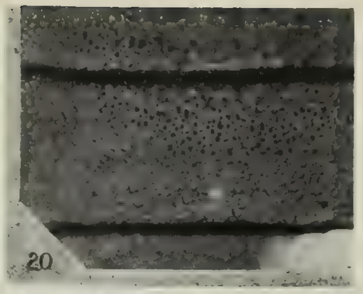
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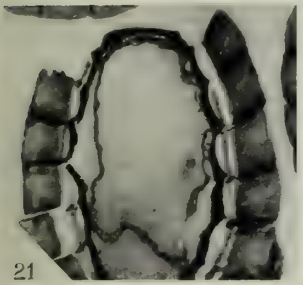
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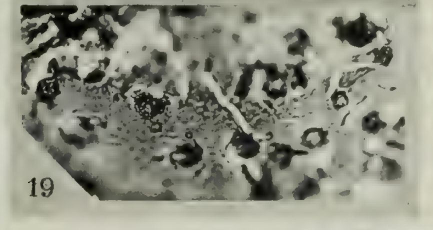
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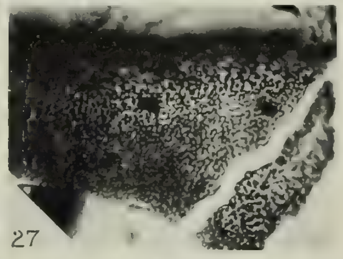
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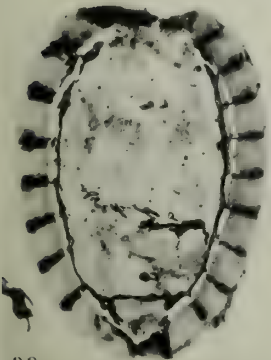
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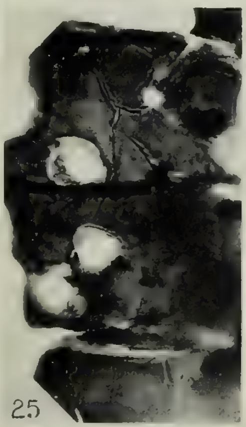
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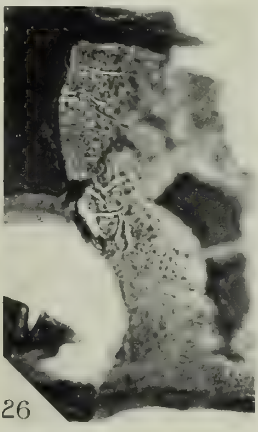
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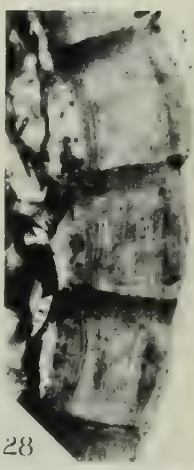
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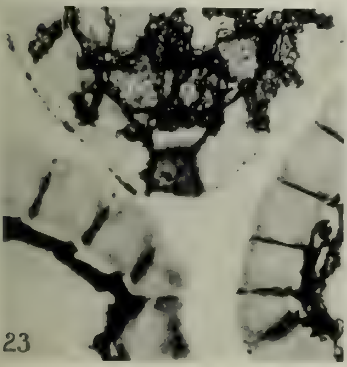
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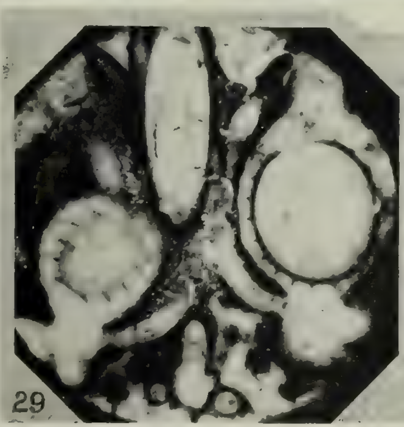
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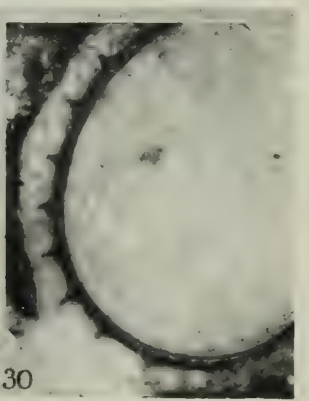
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TROCHILISCUS, LAGYNOPHORA, CHARA

BRITISH MUSEUM NATURAL HISTORY

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PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
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CRETACEOUS AND TERTIARY FORAMINIFERA FROM THE MIDDLE EAST

T. F. GRIMSDALE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 1 No. 8
LONDON : 1952

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BY

THOMAS FRANCIS GRIMSDALE

BRITISH MUSEUM NATURAL HISTORY

Pp. 221–248; *Pls.* 20–25; 3 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in 1949, is issued in five series, corresponding to the Departments of the Museum.*

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PRINTED BY ORDER OF THE TRUSTEES OF
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Issued May 1952 *Price Ten Shillings*

CRETACEOUS AND TERTIARY FORAMINIFERA FROM THE MIDDLE EAST

By T. F. GRIMSDALE

(*With Plates 20–25*)

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SYNOPSIS

One new species is described and figured of each of the following genera: *Articulina*, *Austrotrillina* (?), *Heterillina*, *Idalina*, *Laffitteina*, *Saudia*, and a new variety of *Eorupertia incrassata* (Uhlig). Notes and figures of previously described species are also given.

A brief account of the stratigraphic occurrences and associated faunas of these species provides a background for the descriptive notes. Five of the species are from the Oligocene, seven from the Eocene, two from the Paleocene, and one from the Upper Cretaceous.

I. ACKNOWLEDGEMENTS

I WISH to thank the Iraq Petroleum Company Limited for permission to publish these notes. More particularly, I am happy to acknowledge valuable help from colleagues on the Company's staff: Mr. G. F. Elliott kindly assisted in compiling plates and in checking the draft; Mr. A. H. Smout has discussed with me details of many species; Miss M. Seward has photographed a number of the specimens; and Dr. F. R. S. Henson made a point of insisting upon the publication of my manuscript names, and is, therefore, the moving spirit behind this account. I also wish to thank Mr. C. D. Ovey and Mr. F. M. Wonnacott of the British Museum (Natural History) for assistance in preparing the typescript for the press.

II. INTRODUCTION: FAUNAL ASSOCIATIONS OF SPECIES HERE DESCRIBED

The fifteen species here described do not comprise a single fauna, but are disposed over the sequence from Senonian to Oligocene; however, in most instances they form significant elements of faunas whose other components have been previously recorded. The following introductory notes will serve to indicate the significance of some of the species by discussing the faunas with which they are associated.

A. OLIGOCENE SPECIES

1. *Heterillina hensoni* sp. nov. and *Austrotrillina* (?) *paucialveolata* sp. nov. These two species occur in abundance and are important additions to a fauna, other elements of which have been described by Henson (1950), namely, *Archaias operculiniformis* Henson, *Peneroplis glynnjonesi* Henson, and *Praerhapydionina delicata* Henson.

This fauna occurs in limestone, with abundant Miliolidae, in wells at Kirkuk, Iraq. It underlies beds with *Austrotrillina howchini* (Schlumberger), *Peneroplis thomasi* Henson, and *Praerhapydionina delicata* Henson; and it overlies beds with *Nummulites fichteli* and *N. intermedius* of Lower Oligocene age.

2. *Nummulites vascus* Joly & Leymerie var. *semiglobulus* (Doornink). This form commonly accompanies *Nummulites fichteli*, *N. intermedius*, and *N. vascus* in the Oligocene of Kirkuk.

3. *Nummulites bouillei* de la Harpe. Known from the lowest beds of the Oligocene in Kirkuk.

4. *Lepidocyclina ephippioides* (Jones & Chapman). This species occurs at Kirkuk in beds with *Nummulites fichteli*, *N. intermedius*, and *Lepidocyclina dilatata* (Miche-

lotti), but the two Lepidocyclinae range into younger beds than the *Nummulites*, though still within the Oligocene, while *L. dilatata* at least continues into the Aquitanian.

B. Upper Eocene Species

1. *Spiroclypeus anghiarensis* (Silvestri). This species is associated with *Pellatispira madaraszi* (Hantken) in Kirkuk, and elsewhere with *Nummulites fabianii* Prever and other Upper Eocene forms. For instance, at Maaloula, north-west of Damascus, it occurs with the following fauna:

Asterigerina rotula (Kaufmann)
Asterocyclina sp.
Actinocyclina radians (d'Archiac)
Globorotalia cerroazulensis (Cole)
Hantkenina alabamensis Cushman
Nummulites fabianii Prever
Tubulostium cf. *spirulaea* (Lamarck)
Echinocyamus nummuliticus Duncan & Sladen
Almaena sp. nov.

and a rich fauna of small foraminifera.

2. *Asterigerina rotula* (Kaufmann). Occurs with the foregoing in the Upper Eocene, but ranges down into the Middle Eocene with *Nummulites perforatus*. It is a useful guide species often found entire in well cuttings, whereas the larger nummulites are generally broken.

C. Middle Eocene Species

1. *Nummulites perforatus* (de Montfort) var. Abundant in the Middle Eocene of Kirkuk, in association with *Nummulites discorbinus* (Schlotheim), *Alveolina elliptica* (Sow.), *Orbitolites complanatus* Lamarck, and *Fabiania cassis* (Oppenheim).

2. *Eorupertia incrassata* (Uhlig) var. *laevis* var. nov. Associated with many well-known Middle Eocene species, this variety is readily recognized in thin sections, and forms a useful small guide species which may be encountered entire in drill cuttings, in contrast with the larger nummulite species which are generally broken.

3. *Articulina amphoralis* sp. nov. Found in great abundance in an Eocene limestone in the southern desert of Iraq, about 160 miles west-south-west of the town of Basra. The associated fauna comprising *Peneroplis damesini* Henson, *Praerhapydionina huberi* Henson, and *Meandropsina williamsoni* (Henson) suggests a Middle Eocene age, though Upper Eocene is not excluded.

D. Lower Eocene Species

1. *Laffitteina vanbelleni* sp. nov. The range of this species as established to date is rarely known to overlap the ranges of *Nummulites discorbinus*, *Eorupertia incrassata* var. *laevis*, and *Fabiania cassis* on the one hand, or of *Heterostegina* cf. *ruida* and *Sakesaria cotteri* Davies on the other. It is found in one locality associated with

Nummulites planulatus (Lamarck) var. On the strength of these facts it is regarded as of Lower Eocene age—probably at the top of the Lower Eocene, but this is not yet proven. Its small size and strongly characteristic appearance in thin section make it ideal for correlation in drill cuttings.

2. *Heterostegina* cf. *ruida* Schwager. This species is believed to be of Lower Eocene age from its association with *Sakesaria cotteri* Davies and *Alveolina globosa* Leymerie, in beds lacking any of the conspicuous Paleocene forms listed below.

E. Paleocene Species

1. *Saudia labyrinthica* sp. nov. This species occurs in the following associations:

(*a*) Jebel Sinjar, Iraq. 'Sinjar Limestone.'
Alveolina globosa Leymerie
Alveolina ovulum Stache *in* Schwager
Alveolina cf. *primaeva* Reichel
Gen. nov., sp. nov. Smout, in press
Idalina sinjarica sp. nov.
Miscellanea miscella (d'Archiac & Haime)
Miscellanea stampi Davies
Opertorbitolites sp.
Rotalia cf. *trochidiformis* Lamarck
Saudia labyrinthica sp. nov.

(*b*) Bazian Pass, Iraq.
Alveolina globosa Leymerie
Assilina dandotica Davies
Gen. nov., sp. nov. Smout, in press
Miscellanea miscella (d'Archiac & Haime)
Ranikothalia nuttalli (Davies)
Ranikothalia sindensis (Davies)
Ranikothalia thalica (Davies)
Sakesaria cotteri Davies
Saudia labyrinthica sp. nov.

The 'Ranikot' aspect of the latter assemblage, and the species common to both, have influenced me in assigning them to Paleocene; the possibility of a Lower Eocene age must, however, be entertained.

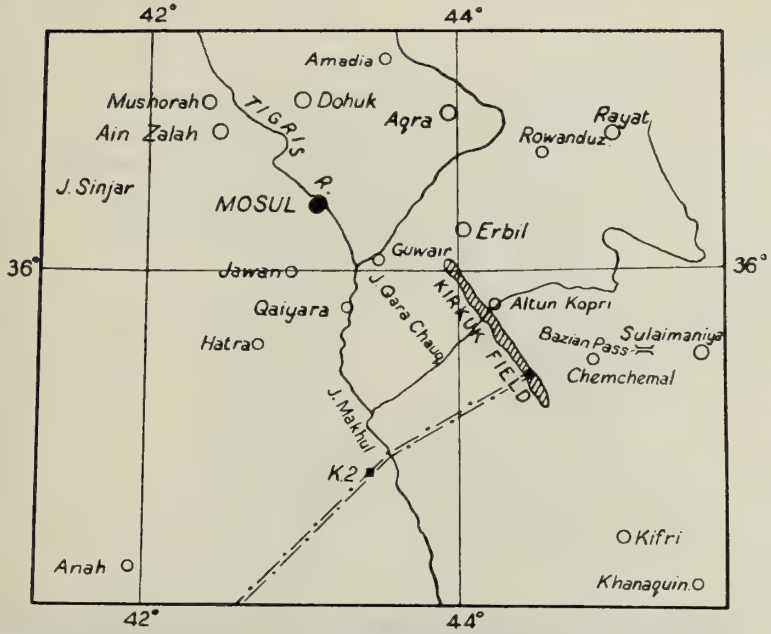
2. *Idalina sinjarica* sp. nov. This species has only been found at Jebel Sinjar.

F. Upper Senonian Species

Monolepidorbis douvillei Astre is believed to have existed prior to the *Omphalocyclus–Orbitoides–Siderolites* fauna of the Maestrichtian.

Most of the localities at which the various species are found may be seen on the map, Text-fig. 1.

The types and a representative series of specimens have been deposited in the British Museum (Nat. Hist.); Museum registration numbers are cited under each species.


42°
44°
Amadia
Mushorah
Dohuk
TIGRIS R.
Ain Zalah
Aqra
Rayat
Rowanduz
J. Sinjar
MOSUL
Erbil
Guwair
36°
Jawan
Qaiyara
J. Qara Chauq
KIRKUK FIELD
Altun Kopri
Bazian Pass
Sulaimaniya
Hatra
Chemchemal
J. Makhul
K.2
Kifri
Anah
Khanaquin
42°
44°

Text-fig. 1. Map showing the localities from which the fossils were obtained.

III. SYSTEMATIC DESCRIPTIONS

Family MILIOLIDAE

Genus *ARTICULINA* d'Orbigny 1826

Articulina amphoralis sp. nov.

(Pl. 21, figs. 5–7; Pl. 23, figs. 9, 12–16)

Material. P. 40634–40645, P. 40710–40715.

Description. Test consisting of a coiled triloculine initial portion followed by a uniserial stage up to 5 chambers long, chamber walls longitudinally costate throughout. Serial chambers rather variable in shape, typically truncate-pear-shaped, but sometimes barrel-shaped, globose or elongated; the later chambers larger than the earlier ones. Aperture single, terminal, rounded or possibly stellate in shape, with a slight neck; the stellate appearance may be restricted to the intercameral foramina, or may be the inner part of a vestibular structure, but its existence is undoubted. It appears to be intimately connected with heavy internal fluting of the portions of the chambers adjacent to the intercameral necks.

Dimensions. (Maximum) length (5 serial chambers) 3·5 mm.; diameter of a serial chamber, 1·1 mm.; diameter of initial coiled portion, 0·88 mm.

Distribution. Abundant in an Eocene limestone in southern Iraq; associated fauna suggests either Upper or Middle Eocene. Type locality, near Chabd; lat. N. 29° 59′ 25″, long. E. 45° 16′ 30″, with *Peneroplis damesini* Henson, *Praerhapydionina huberi* Henson, *Meandropsina williamsoni* (Henson).

Remarks. Articulina amphoralis is larger and more robust than any other species of the genus so far described, and its chambers are typically less elongated than those of any other costate forms of the same genus, e.g. *A. nitida* d'Orb., *A. gibbulosa* d'Orb., *A. sagra* d'Orb., *A. conicoarticulata* (Batsch), *A. antillarum* Cushman, *A. terquemi* Cushman, &c. A few extreme variants in the populations of *A. amphoralis* have rather elongated chambers, but there is intergradation with the typical form; and specimens of these aberrant shapes are so few that no separate variety for them is considered justifiable.

I am indebted to Dr. F. R. S. Henson for part of the foregoing description, adapted from his unpublished manuscript.

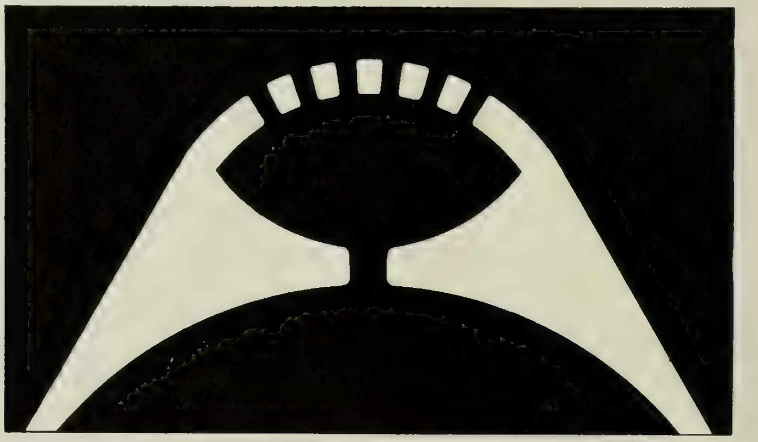
Genus ***HETERILLINA*** Munier-Chalmas & Schlumberger, 1905

Heterillina hensoni sp. nov.

(Pl. 20, figs. 1–6; Text-figs. 2, 3)

Material. P. 40679, P. 40680 (i, ii), P. 40682.

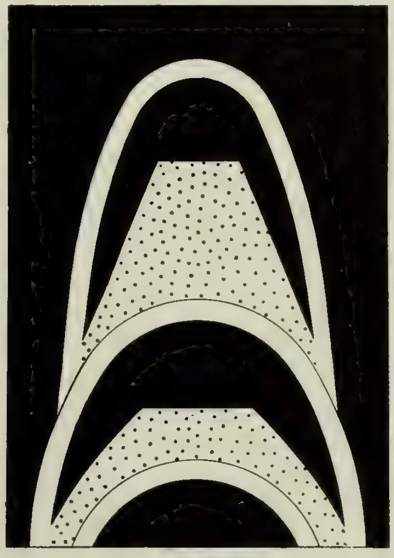
Description. Test smooth, rather thick-walled, roughly circular, compressed, the individual chambers bulging. The early chambers are arranged in a quinqueloculine spiral; the later chambers are only two to a whorl and added in one plane, as in *Massilina*. Each chamber, however, has secreted a chamber wall complete on the inside as well as on the outside; on the inside it has formed a pronounced 'Platform', projecting into the chamber. Often there appear to be cavities between the inner wall of the later added chamber and the former outer wall of the preceding whorl. The aperture seems to be vestibular, with a trematophore, or perforated plate, covering a simple opening at the end of the last chamber.



Text-fig. 2. Diagrammatic reconstruction of a longitudinal section through the aperture of *Heterillina hensoni* sp. nov., to show the inferred vestibular lumen within the trematophore.

Dimensions. Average of numerous specimens from Kirkuk wells K. 14, K. 18, K. 86. Diameter, 2·5 mm.; thickness, 0·75 mm.

Distribution. Miliola Limestone of Kirkuk field, in the Oligocene, where it is associated with *Austrotrillina* (?) *paucialveolata* sp. nov., *Archaias operculiniformis* Henson, *Peneroplis glynnjonesi* Henson, and *Praerhapydionina delicata* Henson.



TEXT-FIG. 3. Diagrammatic transverse section through two chambers of *Heterillina hensoni*, to show thickened inner walls of chambers forming 'platform'.

Remarks. The 'platform' is similar to the structure figured by Schlumberger in *Pentellina strigillata*. *Heterillina hensoni* somewhat resembles *H. guespellensis* Schlumberger, but lacks the surface ornament of that species; no 'platform' is figured in *H. guespellensis*.

Genus *AUSTROTRILLINA* Parr, 1942

Austrotrillina (?) ***paucialveolata*** sp. nov.

(PL. 20, FIGS. 7–10)

Material. P. 40681, P. 40689 (i, ii).

Description. Test ovate in longitudinal, sub-triangular in transverse section. Chambers added as in *Quinqueloculina*, which it resembles in all but the wall structure which is alveolar, the alveolae being coarser and less regular than in *Austrotrillina howchini*. Furthermore, a definite platform, or thickened inner wall, is sometimes visible, as noted in *Pentellina* by Schlumberger, and well developed in *Heterillina hensoni* sp. nov. as described above.

Dimensions. Length of test up to 2·5 mm.; width up to 1·25 mm.

Distribution. In the Miliola Limestone of Kirkuk oilfield, where it is associated with *Heterillina hensoni* and other species. Oligocene.

One of the specimens figured by Silvestri as *Trillina howchini* (1937, pl. 5, fig. 2), from Gotton, Somaliland, is probably this species; this locality is termed Miocene by Silvestri, but he adduces no supporting evidence for this age.

Genus ***IDALINA*** Munier-Chalmas & Schlumberger, 1884

Idalina sinjarica sp. nov.

(PL. 20, FIGS. 11–14)

Material. P. 40672 (ii), P. 40706–40708.

Description. Test almost spherical in some specimens, but generally slightly longer in apertural than in transverse section. The early chambers show quinqueloculine coiling, reduced to biloculine in the adult; but the thickening of the inner walls of the chambers—resembling flosculinization—differentiates the species from a normal *Pyrgo*, though the coiling is similar. The inner, or flosculinized, wall of a chamber is normally at least 5 times as thick as the outer wall. The aperture is vestibular, with what may be a trematophoric plate covering a simple opening, at the end of the test, in the last chamber. No microspheric example has been observed, but one specimen (diameter 2·74 mm. plus) is so far beyond normal size that its microspheric character is suspected, though not determinable.

Dimensions. Maximum diameter 2·74 mm. plus (? microspheric). Average diameter of 8 known megalospheric individuals 1·3 × 1·4 mm. Two well-grown individuals showed dimensions of 1·63 × 1·63 mm. (transverse section) and 2·03 × 1·55 mm. (longitudinal section). Average diameter of nucleoconch 0·165 mm. (8 individuals). Normal wall thickness 0·025 to 0·030 mm. Flosculinized inner wall 0·125 to 0·2 mm.

Distribution. Paleocene limestone of Jebel Sinjar, north-west Iraq.

Remarks. There appear to be only two previously described species of *Idalina*, from both of which *I. sinjarica* differs, as follows: from *I. berthelini* Schlumberger (1905) in lacking striate ornament; from *I. antiqua* d'Orbigny (1884), principally in possessing much heavier thickening of the inner chamber walls. In both described species the initial chamber of the megalospheric generation is recorded as of considerably larger diameter (*I. antiqua*, 0·18 mm. to 0·44 mm.; *I. berthelini*, 0·23 mm. average) than has been found in the present species.

Family PENEROPLIDAE

Genus ***SAUDIA*** Henson, 1948

Saudia labyrinthica sp. nov.

(PL. 21, FIGS. 1–4; PL. 22, FIGS. 1, 2)

Material. P. 40646–40649, P. 40672 (i).

Description. Test compressed, biconcave, circular or oval, flat or somewhat undulating. Growth in the megalospheric form is annular throughout; details of the early stages in the microspheric form are unknown. The individual chambers of the annular portion are subdivided, but incompletely in that partitions do not break the continuity of the annular chamber to form chamberlets.

The external shell layer or epidermis is extremely thin, and is succeeded internally by a 'subepidermal layer' consisting of alveolar cellules formed by annular and radial partitions. Immediately within the epidermis the cellules are irregular, but are succeeded inwards by fairly regular square cellules, two radially per annular chamber, the radial partitions being staggered. Within the subepidermal layer lies a narrow zone in which the annular chambers are unpartitioned, wherein may be seen numerous stolons connecting each chamber with the two adjacent (proximal and distal) annulae; the stolons are at rather regular intervals.

Succeeding this 'open zone', and occupying up to $\frac{9}{10}$ths of the total thickness of the test, is a 'labyrinthic zone', consisting of a mass of shell substance riddled with irregular passages and channels, radial, annular, and transverse, of which the radial are the most continuous and persistent. the annular and transverse being for the most part short and discontinuous.

The 'labyrinthic zone' has evidently developed from a series of pillars and buttresses connecting the annular walls of the chambers, since it thickens distally from a mere median layer of pillars near the nucleoconch to occupy most of the thickness of the test peripherally in adult specimens; the epidermis, the 'subepidermal layer', and the 'open zone' remain constant in thickness from the earliest annuli to the periphery.

As a result of this labyrinthic structure, the continuity of individual chambers and chamber walls is lost in the equatorial layer of the test. Communication with the exterior was probably achieved by numerous apertures on the peripheral face of the outermost chamber, but these have not been actually observed, and their arrangement is therefore unknown.

Dimensions. Diameter: maximum 21 × 16 mm., other specimens of 6·5 mm., 7 mm., 9 mm., 10 mm. Thickness at edge, 0·6 mm. to 1·23 mm. Subepidermal alveolae, from 0·02 to 0·035 mm. About 13 annular chambers occupy 1 mm., measured along a radius. Diameter of megalospheric nucleoconch, about 0·5 mm. Thickness of epidermis, 0·005 mm. approx. Thickness of subepidermal layer, 0·040 to 0·050 mm. approx.

Distribution. Paleocene of Iraq.

Remarks. There is a general resemblance between *Saudia labyrinthica* and *Orbitopsella praecursor* (Gümbel), only the latter lacks the finely cellular subepidermal layer. The species *Orbitolites pharaonum* Schwager (1883) deserves re-study, since there is a similarity between Schwager's inadequate figures and *Saudia labyrinthica* which may not be due to homoeomorphy since both occur at horizons low in the Paleogene.

Saudia labyrinthica differs from *S. discoidea* Henson in one respect only, namely, the immense distal thickening of the equatorial layer; *S. discoidea* shows a similar but much less pronounced increase in thickness peripherally.

Family NONIONIDAE

Genus ***LAFFITTEINA*** Marie, 1946

Laffitteina vanbelleni sp. nov.

(PL. 22, FIGS. 3–11)

1949 *Elphidium* sp. 1: Cuvillier & Szakall, p. 92, pl. 31, fig. 21 (5 views).

Material. P. 40677 (i, ii), P. 40678, P. 40690–40694.

Description. Test planispiral or almost so, of about 2½ whorls, stoutly lenticular to subglobular, margin subacute or rounded. The external surface is coarsely reticulate, the reticulations being formed by the walls of canals which open to the surface; over the centre of the test these canals are normal to the surface, but over the chambers of the embracing outer whorl they are oblique and display a chevron design, following the sutures, which may be observed sometimes on the external surface of the test or in sections close to the surface; this appears to be due to their diverging from their origin in the intraseptal canal system.

The chambers are equitant, but the alar prolongations do not extend far towards the poles, thus leaving a wide umbilical area which is filled with shell material, but spongy with radial canals. The aperture has not been observed, but normal intercameral foramina, at the inner ends of the septa as in *Nummulites*, seem to be present. There are from 14 to 16 chambers in the last whorl of a fully grown specimen.

As stated above, the radial canals which are so characteristic of the species seem to originate in the intraseptal canals. The latter merge proximally, and perhaps distally, in a spiral canal which presumably follows the marginal cord, though on this point precise observation is lacking.

Dimensions. Diameter about 1·5 mm. Thickness about 0·7 mm. Diameter of radial canals, 0·01 to 0·03 mm.

Distribution. In shallow-water limestones of Lower Eocene age in northern Iraq and in Syria; also in the Lower Eocene clays of Gan, south France.

Remarks. Marie (1946) describes the genus *Laffitteina* as being characterized by bilateral asymmetry; in *L. vanbelleni* this is not certainly observable, and if present is very slight. *Laffitteina vanbelleni* differs from *L. bibensis* Marie—the genotype species—in possessing fewer whorls, and fewer chambers per whorl, at a comparable diameter. In vertical sections the two species show remarkable resemblance to one another, and it is possible that *L. vanbelleni* is indeed merely the megalospheric form of *L. bibensis*. The stratigraphic implications of such an identity are interesting, since *L. vanbelleni* cannot possibly be older than Lower Eocene in its known occurrences, while the 'Calcaire pisolithique' of the Paris basin—whence comes *L. bibensis*—is reputed to be of Paleocene age.

Lastly, I am dissatisfied with Marie's reference of his genus *Laffitteina* to the family Nonionidae, but reluctant to propose any alternative. Its most striking resemblances are to *Elphidium* on the one hand and to *Pellatispira glabra* Umbgrove on the other, but close relationship with either will be difficult to prove.

Family NUMMULITIDAE

Genus ***NUMMULITES*** Lamarck, 1801

Amongst the vast literature of the nummulites, with its plethora of specific and varietal names, one finds a relatively small number of basic types appearing over and over again. These 'basic species' may frequently be distinguished from one another without resort to numerical or statistical examination, and sometimes even a single specimen is sufficient for identification. On the other hand, it may be possible to perform, perhaps in a single population of specimens basically alike, a separation into two or more collections distinguishable from each other by some observable minor distinction; these collections may either be rather sharply different—in any particular assemblage under examination—or they may be linked by a complete series of gradational forms. However, no two populations, unless stratigraphically and geographically close, are likely to provide precisely similar sub-populations. If each sub-population is to constitute a separate species, then the number of species will tend to approach or even to exceed the number of populations examined. This is what has happened all too frequently, though not invariably, so that we are burdened with a great number of species of extremely unequal worth, since some are based upon much narrower standards of discrimination than others. In fact, this is but another aspect of the old quarrel—'Lumpers' versus 'Splitters'.

The view is taken here that for a practical stratigraphic approach, the 'lumpers'' attitude is more likely to yield valid results if it be remembered that the wider interpretation of species will connote a longer geological range as well as a wider geographical range. This sounds equivocal, since a short geological range is generally a desideratum from the point of view of the stratigrapher; but where the geographical range is also small—as is frequently the case with the narrowly interpreted species of the 'splitters', in many cases confined to a very limited area indeed—the correlative value is proportionately reduced.

If these 'splitters' species' be regarded as mere races, of geological or geographical significance, then, within the wider geological range of the 'lumpers'' species, such races may be proved to have a locally restricted geological range; but their conspecificity may be valuable in a more than local sense.

In other words, if species *a*, *b*, and *c* are described from three different areas, nothing is added to our knowledge except that species *a* occurs at *X*, species *b* occurs at *Y*, and species *c* at *Z*. But if these three species be recognized as local races of the well-known Upper Eocene species *P*, then we have a strong presumption in favour of an Upper Eocene age for localities *X*, *Y*, and *Z*.

The foregoing provides a key to the interpretations of two of the three Nummulites recorded below. It applies with similar force to *Lepidocyclina ephippioides*, and in fact to almost any fossil organisms of great but finite variability and wide geographical distribution.

Nummulites bouillei de la Harpe

(Pl. 24, figs. 9–11)

1879 *Nummulites bouillei* de la Harpe, p. 60.
1879*a* *Nummulites bouillei* de la Harpe, p. 142, pl. 1, fig. I, 1–3.
1879*a* *Nummulites tournoueri* de la Harpe, p. 143, pl. 1, fig. II, 4–7.
1911 *Nummulites bouillei* de la Harpe: Boussac, p. 45, pl. 5, fig. 4 (useful synonymy).
1935 ? *Nummulites bouillei* de la Harpe: Cizancourt, p. 756, pl. 46, fig. 4.

Material. P. 40669, P. 40671, P. 40673.

Dimensions of Kirkuk specimens. Diameter, maximum 5·0 mm., minimum 3·0 mm. Diameter of nucleoconch, about 0·15 mm. 28–32 chambers in 6th whorl of B-form.

Remarks. I have figured some specimens from Kirkuk, which agree reasonably well with the type description, though the curvature of the septa is greater than is indicated in de la Harpe's rather stylized figures; they are, however, what Boussac describes as 'arquées plus ou moins brusquement dans leur partie périphérique'.

I am inclined to suspect that Mme de Cizancourt's figure (1935) represents an *Operculina*; her neglect to illustrate the critical transverse section must leave this unsettled.

Distribution. Widespread in Europe and the Middle East, in Upper Eocene and Oligocene.

Nummulites perforatus (Montfort) var.

(Pl. 25, figs. 3–9)

1808 *Egeon perforatus* Montfort, pp. 166–167.
1883 *Nummulites perforata* Orb. [*sic*] var. *uranensis* de la Harpe, opp. pl. 3; pl. 3, figs. 1–3 (Non *Nummulina uroniensis* de la Harpe) em. Heim, 1908, p. 226.
1911 *Nummulites bayhariensis* Checchia-Rispoli, p. 131, pl. 4, figs. 9–11.
1938 *Nummulites lucasi* d'Archiac var. *bayhariensis* Checchia-Rispoli: Flandrin, p. 47, pl. 3, figs. 67–70.
Compare also
1911 *Nummulites perforatus* Montfort: Boussac, p. 66.
1948 *Nummulites perforatus* Montfort: Van Andel, p. 1013, text-figs.

Material. P. 40650–40658, P. 40665 (i), P. 40666, P. 40670, P. 40676.

Description. The two generations differ enormously from one another, agreeing only in their generic characters and in possessing pillars; in fact, only their frequent association, combined with the knowledge that such dissimilar pairs are frequent among the larger and more complex Middle Eocene nummulites, can be cited in favour of assuming their relationship.

The B-form has a rather compressed lenticular test, with filaments which are radiate and 'tourbillonantes' (vortex-like) in the young, tending to become meandrine in the adult. Pillars are usually but slightly expressed on the surface but lie both between and attached to the filaments. The spire consists of chambers which are approximately as long as they are high in the early whorls, but with a tendency to be longer relatively in the later whorls. It resembles that of *N. perforatus* and *N. javanus* amongst others.

The megalospheric form is stoutly lenticular, about $\frac{1}{4}$ or $\frac{1}{5}$ the diameter of the microspheric, and possesses large prominent pillars of which the largest are mostly towards the central umbones of the test and appear on the surface as strong pustules. Where the filaments are visible they appear to form a reticulate mesh with markings on the surface which follow the spire of the inner whorls and link the pillars in an obscurely spiral trend. These reticulations are vaguely similar to those observed in *Nummulites fabianii*, but the two species cannot be confounded with each other on account of the striking difference in size of the megalospheric initial chambers; in general also *N. fabianii* possesses a less bulky and more regular spiral lamina.

In equatorial section the spire of *Nummulites 'bayhariensis'* is approximately similar to that of megalospheric *N. perforatus* or to that of the accompanying microspheric specimens at a comparable size; but there is no very striking characteristic to relate it to one or the other, or to differentiate it markedly from examples of *N. atacicus* with abnormally widely spaced septa—except for the presence of pillars.

Dimensions. B-form: The microspheric examples from Kirkuk show the following dimensions: Maximum observed diameter 2·5 cm. At a diameter of 2 cm. there are approximately 17 whorls, but the twisting of the test will not allow of accurate counts.

A typical example provided the following data:

At radius	of	0·16	cm.,	4	whorls	with	7	chambers	per	quadrant
,,	,,	0·4	,,	8	,,	,,	11	,,	,,	,,
,,	,,	?	,,	9	,,	,,	14	,,	,,	,,
,,	,,	0·6	,,	10	,,	,,	14	,,	,,	,,
,,	,,	?	,,	11	,,	,,	15	,,	,,	,,
,,	,,	?	,,	12	,,	,,	17	,,	,,	,,

The ratio of diameter to thickness varies considerably from about 7:1 to 3·5:1, mostly being about 5:1.

A-form: The megalospheric specimens from Kirkuk have these measurements: Maximum diameter 5·0 mm. for a thickness of about 3·0 mm.; at diameter of 4·5 mm. there are 4 whorls. Septa per whorl, 8–9, 16, 24–28, 32. Diameter of nucleoconch generally from 0·9 to 1·0 mm., but occasionally smaller.

Remarks. The presence in the Middle Eocene of Kirkuk of abundant nummulites assignable to Checchia-Rispoli's species *N. bayhariensis*, in close association with a microspheric form clearly no more than a variety of *N. perforatus*, suggested that these might be megalo- and microspheric forms of a single species or variety The strongly turbinate pattern of the septal filaments of the microspheric partner caused me to regard it at first as a new species, but the appearance of Van Andel's work (1948) with its figures—especially text-fig. 1 of 'Forma B. var. 1'—provided a clue as to its true identity.

Some months later my colleague Mr. A. H. Smout was restudying some of the nummulites and came to the conclusion that *N. bayhariensis* should be regarded as at least a valid variety of *N. perforatus*, since it shows constant features which differentiate it from the typical form of the megalospheric partner in that species. At the same time he discovered that Boussac (1911: 74) had described a variant of *N. perforatus* in the following terms: 'Les *filets* sont susceptibles aussi de très grandes variations ; ils peuvent rester rayonnants et seulement ondulés dans l'adulte, comme dans la race *uranensis* de la Harpe.'

On referring to de la Harpe's figures of *N. perforata* var. *uranensis*, Smout found that the rather diagrammatic drawings of this variety represent a form with turbinate filaments and equatorial section reasonably resembling those of the Kirkuk microspheric examples. This seems to confirm my former conclusion that the Kirkuk nummulites now under discussion are closely related to *N. perforatus*. It remained, then, to decide which name to apply to them, and the question at once arises: 'Does this association of "*N. uranensis*" and "*N. bayhariensis*" which in the Middle Eocene of Kirkuk is a strikingly obvious partnership, constitute a true and constant variety of the species *N. perforatus*, or is it a purely fortuitous concurrence of two particular variants of their respective generations?' The present answer to this question is simply 'We don't know', and it may take many years' observation to provide an answer. For this reason the question of a valid varietal name is left unsolved, but it would be perfectly reasonable to apply one or the other or both—at least in the present state of nummulite nomenclature. The fact remains that, for practical purposes, these forms are quite properly regarded as *Nummulites perforatus* (Montfort) var.

Boussac regards Heim's *N. uroniensis*—ascribed by its author to de la Harpe—as distinct from the latter's *N. uranensis* after which it was named, though the difference is less than specific since he equates *N. uroniensis* with *N. perforatus* (1911: 73).

Distribution. *Nummulites perforatus* has a wide distribution in the Eocene of the Tethyan belt, being known from Spain and Morocco in the West to Java (at least) in the East. The variant termed '*N. bayhariensis*' has been recorded from Algeria, Italy, and Somaliland, and now from Kirkuk, Iraq. The form '*N. uranensis*' was described from Switzerland, its only recorded locality previous to the present examples. The two in association have not yet been cited except at Kirkuk.

Nummulites vascus Joly & Leymerie var. **semiglobulus** (Doornink)

(PL. 24, FIG. 16; PL. 25, FIGS. 1, 2)

1848 *Nummulites vasca* Joly & Leymerie, p. 171, pl. 1, figs. 15–17; pl. 2, fig. 7.
For synonymy see Boussac, 1911, p. 35 (*Nummulites vascus*) and p. 32 (*Nummulites incrassatus*).
1906 *Nummulites* (*Paronaea*) *rosai* Tellini var. *obesa* Parisch, p. 78, pl. 1, figs. 22–24.
1932 *Camerina semiglobula* Doornink, pp. 292, 308, pl. 7, figs. 1–14; text-figs. *d*, *e* on p. 293.

Material. P. 40659–40663.

Description. Exceptionally stout and thick-walled microspheric variants of the group of *Nummulites vascus–N. incrassatus* are seen frequently in the Oligocene of Kirkuk, in association with larger and more compressed lenticular microspheric forms referred to *N. vascus* s.s. The megalospheric partners of these two forms have not been distinguished from one another, being assigned simply to *Nummulites* group *vascus*.

These forms have Eocene homoeomorphs in the group of *Nummulites atacicus* Leymerie, from which they are doubtfully distinguishable by a somewhat inconstant difference in the curvature of the septa.[1] This distinction is unsafe for stratigraphical recognition.

This variety is only recognizable in transverse sections.

Dimensions. Diameter reaching 5 mm., thickness about 3 mm.

Distribution. Oligocene of Kirkuk, Iraq; Upper Eocene of Java; Oligocene of Liguria, Italy.

Remarks. Many records of *Nummulites incrassatus* de la Harpe may refer to this form. *N. rosai* Tellini is placed by Boussac in the synonymy of *N. incrassatus*, and Parisch's variety *obesa*, being a homonym, cannot be employed. Doornink's species is therefore reduced to varietal status to comprise such stout radiate forms as these. It is quite reasonable to expect that, sometime, an earlier name for them may be exhumed from the literature to invalidate that of Doornink.

Genus ***HETEROSTEGINA*** d'Orbigny, 1826

Heterostegina sp. cf. ***Heterostegina ruida*** Schwager

(PL. 24, FIGS. 3–8)

Compare 1883 *Heterostegina ruida* Schwager, p. 145, pl. 29, fig. 6*a–e*.
and 1937 *Heterostegina* cf. *ruida* Schwager: Davies, p. 52, pl. 5, fig. 21.

Material. P. 40674 (i, ii), P. 40675, P. 40698–40700.

Description. Test small, flat, of variable outline from nearly circular to elongate oval; there is a slight central thickening over the initial chamber.

The Iraq specimens here figured resemble Schwager's species fairly closely, as may be seen from the figures and the dimensions; but since the external features are unknown in the Iraq species, comparison is incomplete. Furthermore, the Iraq species exhibits a characteristic which distinguishes it from all other described forms of *Heterostegina*, in that the secondary septa possess distal stolons connecting adjacent chamberlets of the same chamber with one another; while no such feature is described for *Heterostegina ruida* from Egypt, this is no evidence of its absence therefrom.

Dimensions. Diameter up to 2·3 mm. Thickness up to 0·4 mm. at the centre of the test.

Distribution. The type specimens of *Heterostegina ruida* were described from the Libyan stage of Egypt, alleged to comprise Paleocene and Lower Eocene.

Heterostegina cf. *ruida* is recorded by Davies from the Sakesar limestone of the Punjab Salt Range, placed by him in the Laki (Lower Eocene); it is associated therein with species of *Assilina* and *Nummulites*, of *Lockhartia* and *Alveolina*, including *Alveolina globosa*, and with *Sakesaria cotteri*.

The Iraq examples are from the Lower Eocene of Mushorah well No. 1 (N. Iraq), where they are associated in drill cuttings with *Alveolina globosa*, *Sakesaria cotteri*, and species of *Nummulites* and *Orbitolites*.

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[1] In the Oligocene forms the septa in median section tend to be approximately radial for the inner $\frac{1}{2}$ to $\frac{2}{3}$ of their length, being sharply reflexed in the outer portion, until in extreme examples they run almost parallel with the periphery. In the Eocene forms such as *Nummulites atacicus* s.s. the septa are inclined and gently curved throughout their length.

Genus *SPIROCLYPEUS* H. Douvillé, 1905

Spiroclypeus anghiarensis (Silvestri)

(Pl. 24, figs. 12–15)

1907 *Heterostegina anghiarensis* Silvestri, p. 56, pl. 2, figs. 6, 7.

Material. P. 40633, P. 40683 (i, ii), P. 40688 (i, ii).

Description. Test very flattened, with a pronounced central boss on each side of the megalospheric nucleoconch; such a boss is probably lacking from the microspheric form. The megalospheric test consists of two or three whorls, opening very rapidly in a flaring manner. Equatorial section is normal heterostegine, but the available material shows little detail and full description must await better specimens. There are only two or three tiers of lateral chambers which appear in vertical section as lines of 'dashes', since they are extremely low in comparison with the height of the roofs and floors, being less than 0·01 mm. in height.

Dimensions. Maximum diameter at least 4·5 mm. Average diameter of 13 specimens, some incomplete, 2·5 mm. Maximum thickness observed 0·79 mm., measured on a broken specimen of diameter 3·2 mm.

Distribution. Silvestri's types are stated to be from the Tongrian of Arezzo, Italy, but no supporting evidence for this age is adduced in his 1907 paper. In the Middle East, specimens occur in the Upper Eocene of Kirkuk field associated with *Pellatispira madaraszi* (Hantken) and *Discocyclina* sp.; in the Upper Eocene of Maaloula, near Damascus, Syria, associated with a rich fauna of large and small foraminifera; in the Upper Eocene of Jebel Hafit, Oman (Arabia), with *Nummulites fabianii* Prever; and at Cheikh Keuy, Syria.

Remarks. This seems to be the most compressed species of *Spiroclypeus* so far encountered, besides being distinguished from other described species by the extreme narrowness of its slit-like lateral chambers See also note on p. 247.

Family AMPHISTEGINIDAE

Genus *ASTERIGERINA* d'Orbigny, 1839

Asterigerina rotula (Kaufmann)

(Pl. 23, figs. 10, 11; Pl. 24, figs. 1, 2)

1867 *Hemistegina rotula* Kaufmann, p. 150, pl. 8, fig. 19*a–e*.
1868 *Rotalia campanella* Gümbel, p. 650, pl. 2, fig. 86*a–e*.
1883 ? *Asterigerina* ? *lancicula* Schwager, p. 127, pl. 28, figs. *a–d*.
1886 *Pulvinulina rotula* (Kaufmann) Uhlig, p. 193, pl. 3, fig. 5*a–c*; pl. 5, figs. 6, 7.

Material. P. 40665 (ii, iii), P. 40702, P. 40703, P. 40709.

Description. Test approaching hemispherical shape, slightly convex dorsally, extremely inflated ventrally, periphery rounded, surface smooth. The sutures, when visible, are not strongly retrorse nor sharply reflexed dorsally, and on the ventral side they bifurcate approximately half-way between the periphery and the large umbonal plug which is always pronounced. The shell substance of the outer wall is fully perforate. The septa appear almost radial, and in correctly oriented sections are opposed by hook-like counter-septa, reminiscent of those described in *Amphistegina lopeztrigoi* Palmer, *Helicostegina*, and *Eulinderina* (Barker & Grimsdale, 1936: 233 *et seq.*). The aperture lies approximately at the junction of the septal face with the previous whorl, below the periphery.

Dimensions. Diameter of test up to 1·5 mm.

Distribution. Described originally from Switzerland, it is reported by Uhlig from west Galicia (Poland); Schwager's *Asterigerina* ? *lancicula* is from the Mokattam stage of Egypt. The occurrences reported here are from Kirkuk, Iraq (Upper and Middle Eocene), and from near Damascus, Syria, in the Upper Eocene.

Remarks. This species has a vertical section which is highly characteristic in rock slices; the limits of its range have not yet been clearly established, but it seems to be restricted to the Upper Eocene and the upper part of the Middle Eocene.

Family VICTORIELLIDAE

Genus ***EORUPERTIA*** Yabe & Hanzawa, 1925

Eorupertia incrassata (Uhlig) var. ***laevis*** var. nov.

(Pl. 20, figs. 15–21)

Compare 1886 *Rupertia incrassata* Uhlig, pl. 4, fig. 5 only.

Material. P. 40695–40697, P. 40701, P. 40704, P. 40705.

Description. Test coiled, consisting of about 2 whorls, the dorsal or attached side flat or slightly concave, the ventral or free side sub-conical with convex slopes and a small concave umbilicus truncating the summit; the shape approximates to that of a skep (woven straw beehive). The second whorl has from 10 to 12 chambers. The coiling is loose, and although the second whorl more or less embraces the inner whorl on the free side of the test, there appears to be a definite lumen between the whorls into which the chambers open. The last few chambers are usually separated from the surface of attachment and show a tendency to flare on the free side. The surface of the test is coarsely perforate, but almost smooth, lacking the tubercles seen in *Eorupertia incrassata* and other described species of *Eorupertia*; and alternating series of irregularly radiating ridges and slits are seen in the umbilical depression, the slits probably communicating with the internal lumina.

Dimensions. Maximum diameter about 2·5 mm.; height approximately equal to diameter.

Distribution. Iraq, east Arabia, Oman, Turkey; apparently restricted to the Middle Eocene. Specimens from the Upper Lutetian of France (Grande Carrière, Lassalle, Landes; and St. Martin de Hinx, well A, at 37 m.) in the British Museum (Natural History) undoubtedly belong to this variety.

Remarks. The smooth specimen figured by Uhlig (1886) closely resembles specimens from the Iraq Middle Eocene which are consistently smooth, tuberculate ornamentation being exceptional; on this ground the erection of a new variety is believed justifiable.

Family ORBITOIDIDAE

Genus **MONOLEPIDORBIS** Astre, 1928

Monolepidorbis douvillei Astre

(Pl. 23, figs. 1–7)

1906 *Linderina* sp.: H. Douvillé, p. 601, pl. 18, fig. 18.
1928 *Monolepidorbis douvillei* Astre, p. 390.
1936 *Monolepidorbis douvillei* Astre: Reichel, p. 44, pl. 4, figs. 1, 5.
1948 *Orbitoides media* (d'Archiac): Silvestri, p. 84 (156), pl. 7 (15), figs. 4–7.

Material. P. 40684–40687 in the British Museum collections; additional sections in the Iraq Petroleum Company's Geological Research Centre.

Description. Test depressed conical in form, consisting of an equatorial layer of chambers disposed in a flat cone and cyclically arranged about a nucleoconch which appears to be two-chambered and sandwiched between layers of densely perforated shell substance thick over the centre but thinning peripherally. The equatorial chambers appear arcuate in equatorial section; each chamber is connected with adjacent chambers of the previous and subsequent cycles by means of diagonal stoloniferous passages which are circular in cross-section and disposed in two or three tiers—as may be observed in transverse sections. The appearance of transverse sections recalls in all respects—except for the absence of lateral chambers—species of the genus *Orbitoides* rather than of *Lepidorbitoides* or *Lepidocyclina.* The surface ornament has not been observed, but probably consists of pustules, perhaps elongated radially as in *Orbitoides faujasi* and *O. media.*

Dimensions. Average diameter (12 individuals) 1·5 mm. Maximum diameter observed 2·1 mm. Maximum thickness observed 0·62 mm. Equatorial chambers: radial diameter about 0·1 mm. Annular diameter about 0·13 mm. Height 0·1 to 0·15 mm.

Distribution. Originally described from the Campanian of France; specimens here referred to this species abound in the Upper Senonian of Iraq. The examples figured by Silvestri (1948) as *Orbitoides media* purport to be from the Maestrichtian of northern Somaliland.

Remarks. The specimens above described are probably all megalospheric, but the nucleoconch is in no case sufficiently clearly observed to warrant an illustration. It may, however, be stated with certainty that there is no large thick-walled nucleoconch of the type known in *Orbitoides*, but a small two-chambered affair apparently resembling either *Orbitocyclina* or *Lepidorbitoides.*

Genus **LEPIDOCYCLINA** Gümbel, 1868

Lepidocyclina ephippioides (Jones & Chapman)

(Pl. 23, figs. 8, 17, 18)

1900 *Orbitoides* (*Lepidocyclina*) *ephippioides* Jones & Chapman, pp. 251–252, 256, pl. 20, fig. 9; pl. 21, fig. 15.
1900 *Orbitoides* (*Lepidocyclina*) *andrewsiana* Jones & Chapman, p. 255, pl. 21, fig. 14.

1900 *Orbitoides* (*Lepidocyclina*) *insulae-natalis* Jones & Chapman, pp. 242, 256, pl. 20, fig. 5; pl. 21, fig. 13.
1900 *Orbitoides* (*Lepidocyclina*) *insulae-natalis* Jones & Chapman var. *inaequalis* Jones & Chapman, p. 254, pl. 21, fig. 12.
1900 *Orbitoides* (*Lepidocyclina*) *murrayana* Jones & Chapman, pp. 252–253, pl. 21, fig. 10.
1902 *Lepidocyclina formosa* Schlumberger, p. 251, pl. 7, figs. 1–3.
1904 *Lepidocyclina raulini* Lemoine & Douvillé, p. 11, pl. 1, figs. 3, 6, 9, 13, 16; pl. 2, figs. 3, 10; pl. 3, figs. 4, 14; text-fig. 2.
1906 *Orbitoides richthofeni* Smith, p. 205, pl. 1, figs. 1, 2.
1907 *Orbitoides* (*Lepidocyclina*) *inflexa* Checchia-Rispoli, p. 164.
1909 *Orbitoides* (*Lepidocyclina*) *inflexa* Checchia-Rispoli, p. 101, pl. 5, figs. 8, 9.
1909 *Lepidocyclina formosa* Schlumberger: R. Douvillé, p. 135, pl. 6, fig. 1.
1911 *Lepidocyclina* (*Eulepidina*) *inermis* H. Douvillé, p. 72, pl. D, fig. 5.
1911 *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger: H. Douvillé, p. 72, pl. D, figs. 2–4.
1911 *Lepidocyclina insulae-natalis* (Jones & Chapman) H. Douvillé, p. 71, pl. B, figs. 1–3.
1914 *Lepidocyclina sumatrensis* (Brady) var. *inornata* Rutten, p. 294, pl. 22, figs. 6–8.
1915 ? *Lepidocyclina verbeeki* (Newton & Holland) var. *papuaensis* Chapman, p. 297, pl. 8, figs. 5, 6; pl. 9, fig. 10.
1919 *Lepidocyclina crassata* Cushman, p. 61, pl. 11, figs. 4, 5; text-fig. 8.
1919 *Lepidocyclina favosa* Cushman, p. 66, pl. 3, figs. 1*b*, 2; pl. 15, fig. 4.
1919 *Lepidocyclina* (*Eulepidina*) *gibbosa* Yabe, p. 46, pl. 6, figs. 3, 4*c*, 7*c*.
1919 *Lepidocyclina* (*Eulepidina*) *monstrosa* Yabe, p. 42, pl. 6, fig. 5*a*; pl. 7, figs. 11, 12*a*, 13.
1919 *Lepidocyclina* (*Eulepidina*) sp. indet. cfr. *inermis*: Yabe, p. 46, pl. 7, fig. 2.
1919 *Lepidocyclina insulae-natalis* (Jones & Chapman): Yabe, p. 44.
1920 *Lepidocyclina chattahoocheensis* Cushman, p. 65, pl. 23, figs. 1–4; pl. 24, figs. 1, 2.
1924 *Eulepidina formosa* (Schlumberger): H. Douvillé, p. 49, pl. 2, fig. 1.
1925 *Lepidocyclina* (*Eulepidina*) *dickersoni* Yabe & Hanzawa, p. 104, pl. 25, figs. 10, 11.
1925 *Eulepidina formosoides* H. Douvillé, p. 71, pl. 3, figs. 2–4.
1925 *Lepidocyclina* (*Eulepidina*) *richtofeni* (Smith) var. *plana* Yabe & Hanzawa, p. 106, pl. 26, figs. 5–7.
1925 *Lepidocyclina formosa* Schlumberger var. *atuberculata* van der Vlerk, p. 20, pl. 2, fig. 17; pl. 4, fig. 30; pl. 6, fig. 52.
1925 *Eulepidina formosa* (Schlumberger): H. Douvillé, p. 97.
1926 *Lepidocyclina blanfordi* Nuttall, p. 334, pl. 13, figs. 5, 6, 9, 10.
1926 *Lepidocyclina* (*Eulepidina*) *andrewsiana* (Jones & Chapman): Nuttall, p. 27, pl. 4, figs. 1, 4.
1926 *Lepidocyclina* (*Eulepidina*) ? *formosa* Schlumberger: Nuttall, p. 29.
1926 *Lepidocyclina* (*Eulepidina*) *insulae-natalis* (Jones & Chapman): Nuttall, p. 30, pl. 4, figs. 2, 5, 6.
1926 *Lepidocyclina* (*Eulepidina*) *chapmani* Nuttall, p. 31, pl. 4, figs. 7–9.
1926 *Lepidocyclina* (*Eulepidina*) *inaequalis* (Jones & Chapman): Nuttall, p. 33, pl. 4, fig. 3.
1926 *Lepidocyclina ephippioides* (Jones & Chapman): Nuttall, p. 34, pl. 5, figs. 1–3, 8, 10.
1927 *Eulepidina royoi* Gomez Llueca, p. 426.
1929 *Eulepidina royoi* Gomez Llueca, p. 343, pl. 34, figs. 3–5.
1929 *Eulepidina formosoides* H. Douvillé: Gomez Llueca, p. 339, pl. 30, figs. 7–13; pl. 31, figs. 1–3.
1929 ? *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger var. *sella* Zuffardi-Comerci, p. 133, pl. 7, figs. 5, 11.
1930 *Lepidocyclina* (*Eulepidina*) *gibbosa* Yabe: Hanzawa, p. 90, pl. 26, figs. 6–9.
1930 *Lepidocyclina* (*Eulepidina*) *richtofeni* (Smith): Hanzawa, p. 88, pl. 26, figs. 1–5; pl. 27, fig. 11; pl. 28, figs. 1–13.
1930 *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger: Hanzawa, p. 90, pl. 26, fig. 13.
1930 *Lepidocyclina* (*Eulepidina*) *dickersoni* Yabe & Hanzawa: Hanzawa, p. 90, pl. 26, fig. 12.
1932 *Lepidocyclina crassata* Cushman: Scheffen, pp. 32, 33, pl. 6, figs. 1–3.
1933 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Vaughan, p. 37, pl. 17, figs. 1–3; pl. 18,

figs. 1–4; pl. 19, figs. 1–4; pl. 20, figs. 1–3; pl. 21, figs. 1, 3, 4. This paper provides full references and synonymy for the western hemisphere up to 1933.

1934 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Cole, p. 27, pl. 4, figs. 2, 3, 12.

1935 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Rutten M. G., p. 540.

1935 *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger: van de Geyn & van der Vlerk, p. 234.

1937 *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger: Thiadens, p. 105.

1937 *Lepidocyclina zuffardii* Silvestri, p. 199, pl. 13 (10), fig. 6; pl. 20 (17), figs. 10, 11.

1937 *Lepidocyclina favosa* Cushman: Silvestri, p. 189, pl. 18 (15), fig. 4; pl. 19 (16), fig. 5; pl. 20 (17), figs. 8, 9; pl. 21 (18), figs. 5, 6.

1937 *Lepidocyclina formosa* Schlumberger: Silvestri, p. 196, pl. 16 (13), figs. 4, 5; pl. 22 (19), fig. 1.

1937 *Lepidocyclina formosoides* (H. Douvillé): Silvestri, p. 195, pl. 16 (13), figs. 7, 8; pl. 22 (19), fig. 2.

1937 *Lepidocyclina royoi* (Gomez Llueca) Silvestri, p. 191, pl. 18 (15), fig. 5; pl. 19 (16), figs. 2–4; pl. 20 (17), figs. 6, 7; pl. 21 (18), figs. 4, 7.

1937 *Eulepidina dilatata* (Michelotti) var. *insulae-natalis* H. Douv. [sic!]: David-Sylvain, p. 20, pl. 2, fig. 8.

1941 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Vaughan & Cole, p. 75, pl. 40, figs. 1–4.

1942 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Hanzawa & Asano, p. 120, pl. 9, figs. 1–4; pl. 10, figs. 1, 3, 4; pl. 11, figs. 1–5.

1942 *Lepidocyclina* (*Eulepidina*) cfr. *favosa* Cushman: Marchesini, p. 60, pl. 3, figs. 2, 3.

1942 *Lepidocyclina* (*Eulepidina*) *raulini* Lemoine & R. Douvillé: Marchesini, p. 53, pl. 1, figs. 3, 7–9.

1942 *Lepidocyclina* (*Eulepidina*) *formosoides* (H. Douvillé) var. *asimmetrica* Marchesini, p. 56.

1945 *Lepidocyclina* (*Eulepidina*) *favosa* Cushman: Cole, p. 41, pl. 4, figs. 3, 4, 7, 11.

Material. P. 40664, P. 40667, P. 40668.

Description. Test with thick central portion and thin peripheral flange, sometimes clearly demarcated from each other, sometimes continuous with one another forming a lenticular whole. The relative inflation of the central portion is extremely variable, and the test as a whole may be flat or sellate. An external pattern or ornament is formed by reticulate ridges which represent the more or less thickened walls of the lateral chambers; these are always coarser and more apparent near the centre of the test than towards the periphery or on the flange, and in extreme cases resemble the zoarium of a massive cyclostomatous polyzoan.

The equatorial chambers are large, hexagonal, or spatulate; they give the impression of being arranged in cycles. The nucleoconch is eulepidine; the large chamber seems almost entirely to surround the smaller one in correctly oriented equatorial sections. In oblique sections or in sections parallel to, but outside, the equatorial plane this character is not apparent, and there may be a false resemblance to a nephrolepidine nucleoconch.

The lateral chambers have thick walls which may give the impression of strong pillars in axial sections. Oblique sections have been described as showing anastomosing pillars; these illusions are dispelled by observation of tangential sections and exteriors, when it may readily be seen that there are no pillars and that the appearance is due to strong thickening of the walls—normal to the equatorial layer—of the lateral chambers. This thickening, though extremely variable in amount, is most pronounced near the centre of the test; in tangential sections, i.e. sections through the lateral chambers and parallel to the equatorial layer, the thickened walls may be seen in some specimens to equal in diameter the cavities of the chambers. The lateral chambers are of open appearance in vertical sections and their roofs and floors are thin.

Dimensions of Kirkuk examples. Maximum diameter, 18 mm., minimum 3 mm. Diameter of nucleoconch 0·5 mm. to 1·0 mm. Lateral chambers, 9 to 10 in a height of 1 mm. Length in vertical section, 0·1–0·35 mm.

Distribution. This species was originally described from Christmas Island (Indian Ocean), from strata thought to be most probably of Miocene age. However, it has a wide geographic distribution and may be stated quite definitely to occur in rocks of different ages in different places; its migration can be followed about three-quarters round the world.

In the western hemisphere it occurs in Lower and Middle Oligocene, and is recorded from the following countries: Mexico, U.S.A. (Florida), Cuba, Antigua (Leeward Islands), Trinidad; I have seen specimens in the Oligocene of Venezuela.

In Europe it is known from Spain, France, and Italy. Here it is associated with *Nummulites intermedius* (d'Archiac) and *N. fichteli* Michelotti, but ranges probably above the zone of these nummulites.

In the Middle East its occurrence in Kirkuk is in the higher part of and above the beds with *N. intermedius*, but does not range far down in these beds, and is far removed from the base of the Oligocene.

In the Far East it is widely recorded, generally from beds regarded as of Aquitanian or of Miocene age. However, in the latest stratigraphical work on the Philippine Islands (Hashimoto, 1939: 385), the Binangonan limestone is correlated with the Cebu formation of the Visaya Series, which is placed in the Oligocene. Species of *Lepidocyclina* here included in *L. ephippioides* have been recorded from the Binangonan limestone.

Further precise stratigraphical observations on the occurrence of *Lepidocyclina ephippioides* will be necessary to complete the picture; but the impression of migration from Mexico via the Mediterranean and India to the East Indian Islands is inescapable, and this movement occupies at least the whole of the Oligocene.

Remarks. The chequered nomenclatural history of this variable species may be inferred from the foregoing synonymy, which is still incomplete. No doubt it would be possible to prove the existence of local races which might be distinguished as varieties; but examination of material from many parts of the world leaves me convinced that no specific distinctions are valid.

All of the supposed species in the long list of synonyms are based upon variations which are generally found in any assemblage, comprising:

(*a*) Wide variability of ratio between diameter and thickness.
(*b*) Relative development of flange and umbo.
(*c*) Width of lateral chambers and thickening of walls between them.
(*d*) Sellate distortion of the test.

Hanzawa & Asano (1942: 121–123, including table of dimensions) have taken pains to demonstrate certain distinctions between *Lepidocyclina formosa* and

Lepidocyclina favosa, namely, absolute diameter (*Lepidocyclina formosa* is from 2 to 4 times as large as *L. favosa*), and ratio diameter/thickness (see below):

	Megalospheric	*Microspheric*
L. formosa . . .	1·7:1–3·2:1	2:1–3:1
L. favosa . . .	2·2:1–5·7:1	6:1–11:1

(After Hanzawa & Asano.)

This latter divergence between the ratios diameter/thickness would be more convincing if it were not correlated with differences in diameter; or in other words, the young of *Lepidocyclina formosa* may still be indistinguishable from the adult *Lepidocyclina favosa*. Now difference in size could itself be correlated with a difference in the latitude of provenance, could in fact be purely a matter of more or less favourable environment. From this I would infer that distinction between these species is not proven and is better not maintained. There remains, however, the possibility that geographical or stratigraphical races may eventually be found to merit recognition in a varietal status only.

The rules of priority seem to point to *Lepidocyclina ephippioides* as the earliest applicable name of the species, which is therefore adopted here. The Kirkuk specimens would all qualify for inclusion in *Lepidocyclina favosa* rather than in *L. formosa* were the distinction between these species to be upheld.

The fundamental characters of the species—hexagonal or spatulate equatorial chambers, eulepidine nucleoconch, lack of pillars, but thickening of lateral chamber walls visible in varying degree—remain stable amid all the extremities of variation of the remaining characters. *Lepidocyclina ephippioides* resembles *L. dilatata* as far as the equatorial layer is concerned, but differs in not having pillars and in the thickening of the walls of the lateral chambers. In general, it is stouter than *L. dilatata*, but this character is gradational. *Lepidocyclina elephantina* usually possesses 'buried' pillars which fail to reach the surface; the lateral chambers are small and with unthickened walls.

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Note on *Spiroclypeus* (p. 238).

The species *Spiroclypeus vermicularis* Tan, from the Eocene of East Borneo, is certainly identical with or very closely related to the form here described as *S. anghiarensis* Silvestri; but see Tan Sin Hok (1937: 187, pl. 1, figs. 7, 8; pl. 2, figs. 6–10; pl. 3, figs. 13–23; pl. 4, figs. 11–18).

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PLATE 20

FIGS. 1–6. *Heterillina hensoni* sp. nov.

1. Transverse section, cutting the initial chamber: shows inner wall of later chambers strongly thickened to form the 'platform', × 20. Specimen lost.
2. Transverse section of syntype, showing 'platform', × 20. P. 40680 (i).
3. Tangential section of syntype, cutting the aperture, and showing the trematophore, × 30. Specimen destroyed in remounting.
4. Longitudinal section of syntype, cutting the initial chamber, and showing thickening of inner walls of later chambers, × 20. P. 40680 (ii).
5. Oblique section of syntype, cutting the initial chamber, × 20. P. 40679.
6. External view of syntype on rock chip, × 20. P. 40682.

All the above specimens are from the Oligocene of Kirkuk, well 14.

FIGS. 7–10. *Austrotrillina* (?) *paucialveolata* sp. nov.

7. Oblique section of syntype, × 30. P. 40688.
8. Oblique section of syntype, × 30. P. 40689 (i).
9. Tangential section of syntype, showing alveoli near surface of test, × 30. P. 40689 (ii).
10. Transverse section of syntype, which just misses the initial chamber, × 20. P. 40681.

All the above specimens are from the Oligocene of Kirkuk, well 14.

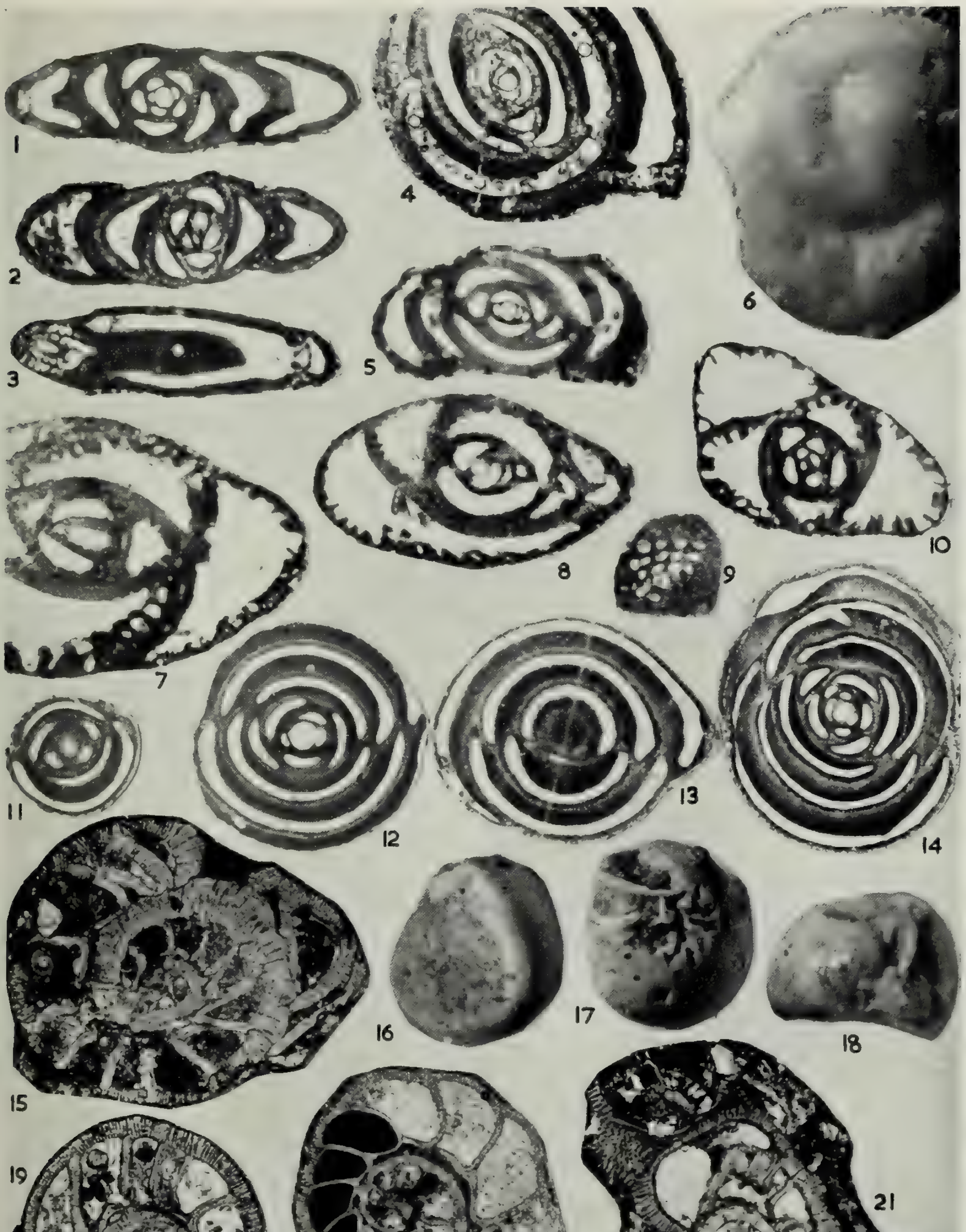
FIGS. 11–14. *Idalina sinjarica* sp. nov.

11. Longitudinal section of small example. The specimen shows what appears to be a vestibular structure at the apertural end of the last chamber (but this is barely visible in the photograph), × 20. Syntype P. 40708.
12. Transverse section of syntype showing initial chamber and early milioline coiling. P. 40706.
13. Longitudinal section, slightly off centre, of syntype. Shows indications of vestibular structure at apertural end of last chamber, × 20. P. 40707.
14. Transverse section, slightly oblique, of syntype; shows quinqueloculine early coiling around initial chamber, × 20. P. 40672 (ii).

All the above specimens are from the Paleocene–Lower Eocene Sinjar Limestone of Jebel Sinjar, N. Iraq.

FIGS. 15–21. *Eorupertia incrassata* (Uhlig) var. *laevis* var. nov.

15. Section, in plane of coiling, of syntype from Ain Zalah, well 1, × 20. P. 40696.
16. External view of dorsal (attached) surface of specimen from a well in Arabia, × 15. P. 40704.
17. External view of ventral side of specimen from a well in Arabia, × 15. P. 40705.
18. Lateral aspect of the specimen seen in Fig. 16, × 15. P. 40704.
19. Oblique section of syntype from Ain Zalah, well 1, × 20. P. 40697.
20. Section, in plane of coiling, of specimen from Ain Zalah, well 1, showing lumen between outer and inner whorls, × 20. P. 40695.
21. Vertical section of specimen from Butmah, well 1, × 20. P. 40701.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MIDDLE EAST FORAMINIFERA

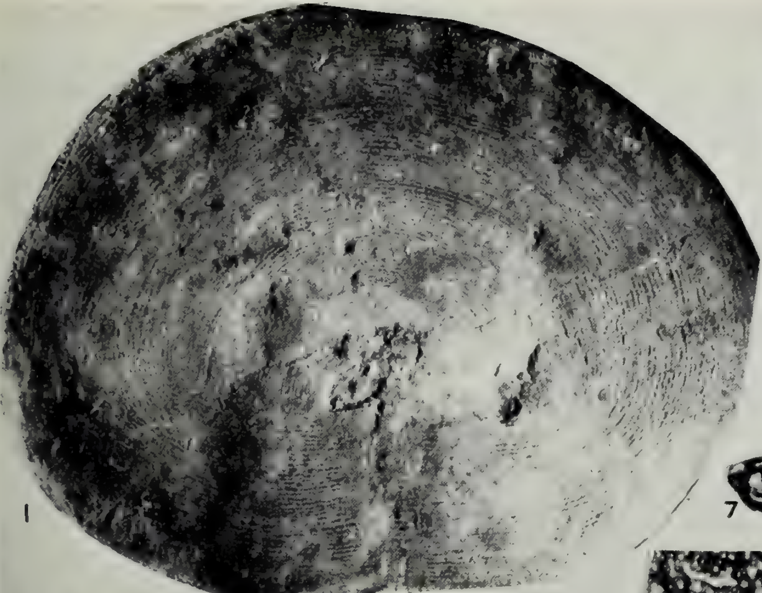
PLATE 21

FIGS. 1–4. *Saudia labyrinthica* sp. nov.

1. External view of a large example from the Bazian Pass, N. Iraq, × 5. P. 40646.
2. Transverse section of the peripheral portion of the specimen seen in Pl. 22, fig. 2, to show detail of the sub-epidermal and labyrinthic layers, × 45. P. 40672 (i).
3. Equatorial section, slightly oblique, to show detail of sub-epidermal layer, 'open zone', and the intercameral (radial) foramina, × 52. (Enlargement of specimen figured on Pl. 22, fig. 1.) P. 40649.
4. Approximately equatorial section through the peripheral portion of a large example, to show the radial passages in the labyrinthic layer. Distal side left; proximal right, × 18. P. 40647.

FIGS. 5–7. *Articulina amphoralis* sp. nov. Longitudinal sections of three examples from Rudhuma, SW. Iraq.

5. Iraq Petroleum Co.'s Geological Museum, × 22. No. M/4132.
6. Shows early coiled stage, × 16. P. 40634 (i).
7. The final 'detached' chamber shows traces of the external ornament of longitudinal costae, × 18. P. 40634 (ii).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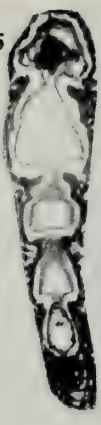
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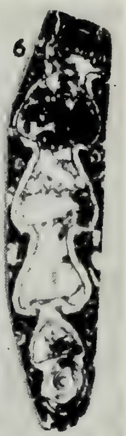
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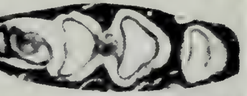
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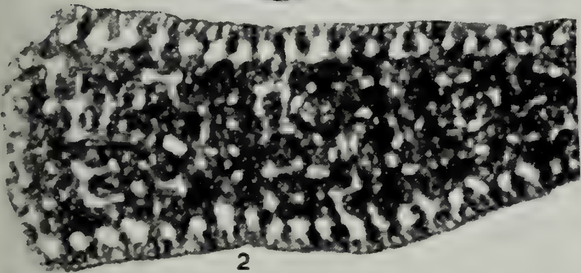
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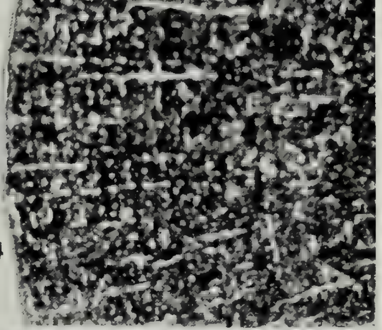
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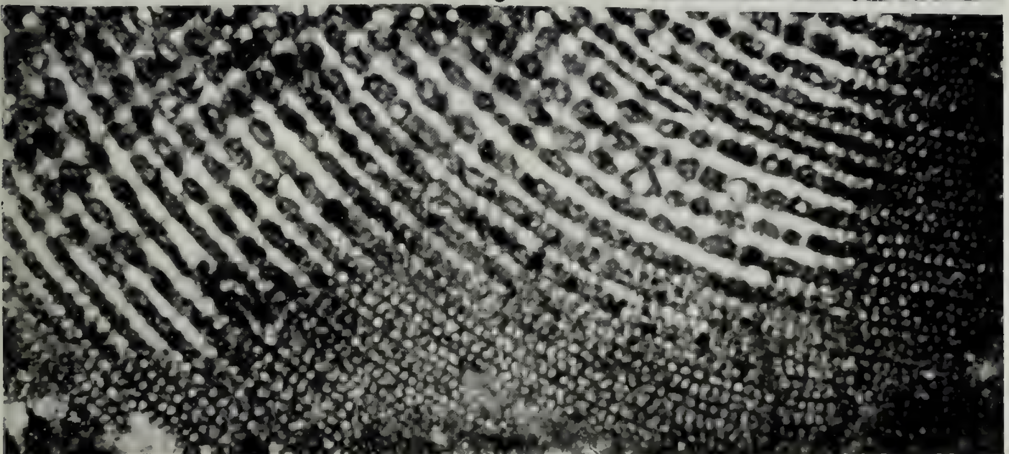
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MIDDLE EAST FORAMINIFERA

PLATE 22

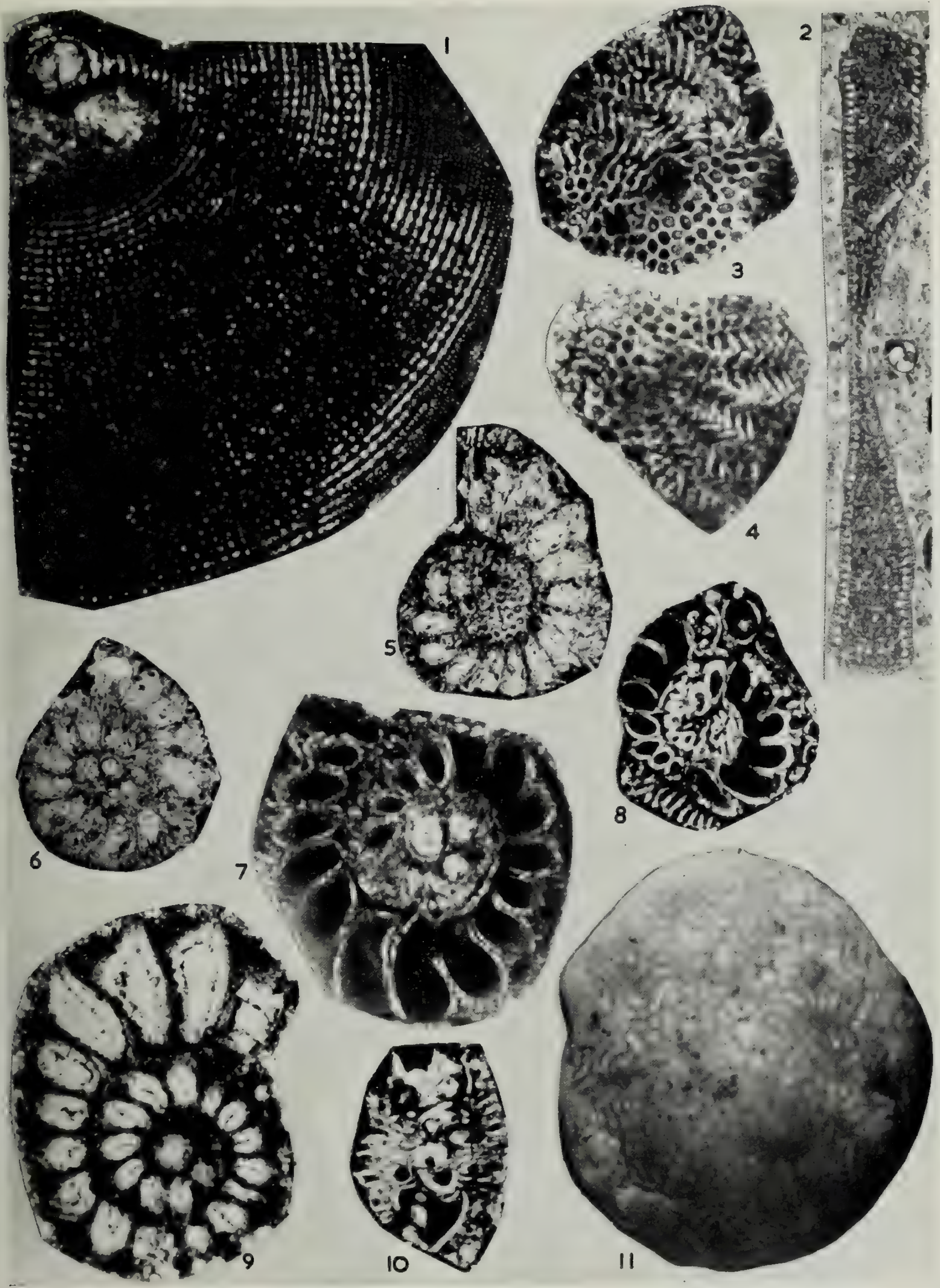
FIGS. 1–2. *Saudia labyrinthica* sp. nov.

1. Equatorial section, slightly oblique, of specimen from the Bazian Pass, N. Iraq, showing the megalospheric nucleoconch and the internal structure. At the right-hand side may be seen the sub-epidermal layer, and in the centre is the median mass of the labyrinthic layer; these two layers are separated by the 'open zone', × 20. P. 40649.
2. Transverse section of specimen from the Paleocene–Lower Eocene Sinjar Limestone of Jebel Sinjar, N. Iraq. Shows loss of continuity of the annular walls and lumina of the chambers in the labyrinthic layer, × 15. P. 40672 (i).

FIGS. 3–11. *Laffitteina vanbelleni* sp. nov.

3, 4. Sections parallel to surface of test, showing vertical canals over umbilical region and divergent canals over the chambers of the outermost whorl, × 40. Both specimens are from Mushorah, well 1. 3, P. 40693; 4, P. 40690.

5. Tangential section parallel to the plane of coiling, × 30. From the Eocene of Kourdane, Syria. P. 40677.
6. Equatorial section from Kourdane, Syria, × 30. P. 40677.
7. Equatorial section from the Lower Eocene of Mushorah, well 1. Shows lumina in septa, × 40. P. 40692.
8. Oblique section from Kourdane, Syria, × 30. P. 40677.
9. Equatorial section of specimen from Mushorah, well 1, × 40. P. 40691.
10. Transverse section of specimen from Kourdane, Syria, × 30. P. 40678.
11. External aspect of specimen from Mushorah, well 1, × 40. P. 40694.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MIDDLE EAST FORAMINIFERA

PLATE 23

FIGS. 1–7. *Monolepidorbis douvillei* Astre.

1. Transverse section which misses the nucleoconch but shows the *Orbitoides*-like stolon passages between chambers of the equatorial layer. The 'pillars' are probably represented by radial costae on the surface, × 3. From Qalian, well 1. P. 40684.
2. Transverse section, × 30. P. 40686.
3. Slightly oblique transverse section, × 30. P. 40687.
4. Oblique section, × 30. P. 40686.
5. Oblique section showing equatorial chambers and stoloniferous passages connecting them, × 30. From Qalian, well 1. P. 40684.
6. Equatorial section. The nucleoconch is not clearly shown, × 30. P. 40686.
7. Equatorial section, × 30. P. 40685.

All the above specimens, except P. 40684, are from Jawan, well 2.

FIGS. 8, 17, 18. *Lepidocyclina ephippioides* (Jones & Chapman).

8. Transverse section by reflected light on polished surface of rock, × 15. Kirkuk, well 19. P. 40664 is a thin section prepared from the same specimen.
17. Specimen cut obliquely on polished rock surface, photographed by reflected light, × 15. Kirkuk, well 19. This specimen was not preserved.
18. Equatorial section, × 10. Kirkuk, well 19. P. 40667.

FIGS. 9, 12–16. *Articulina amphoralis* sp. nov.

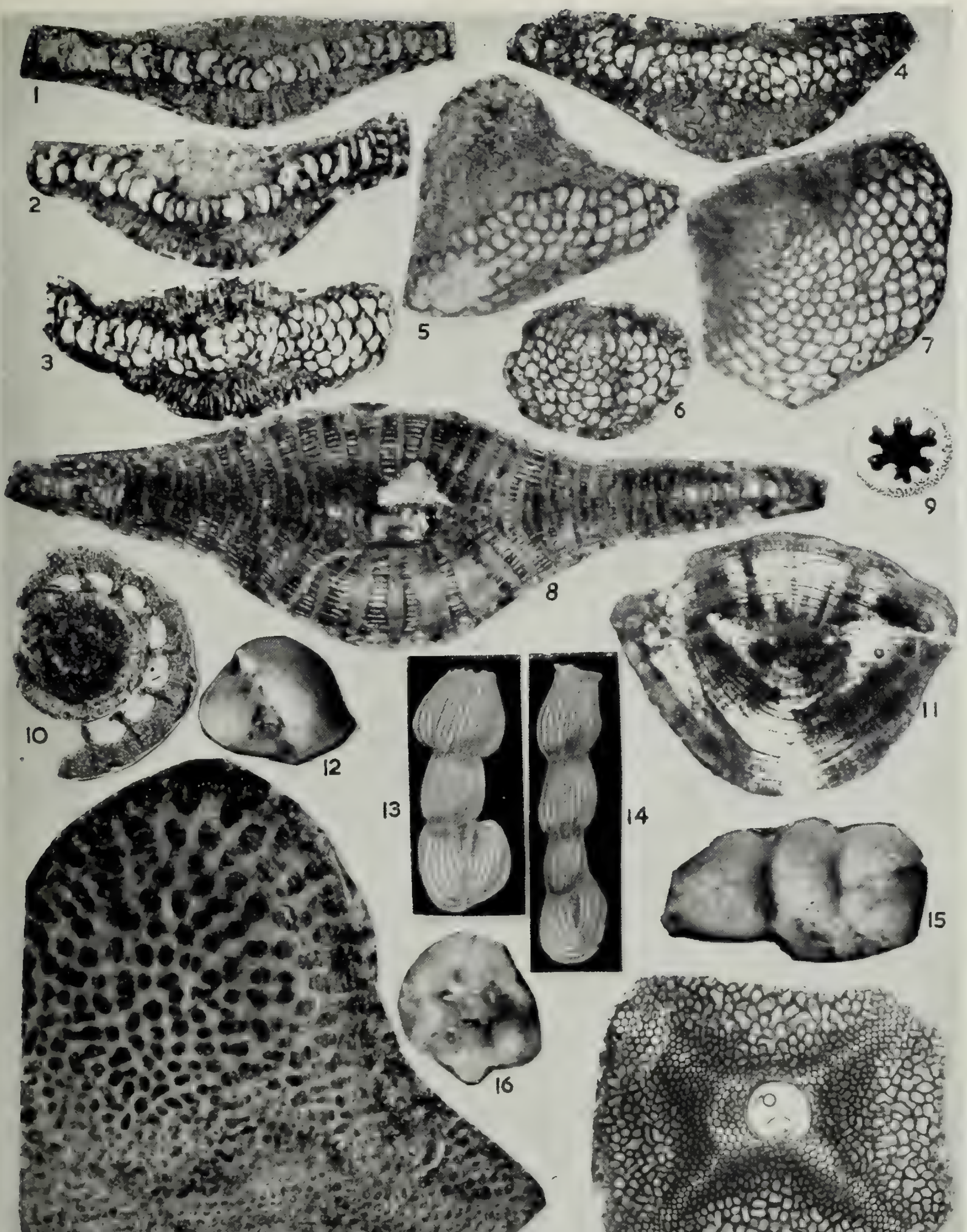
9. Reconstruction of apertural view showing the stellate or fluted character, × 30 approx. Diagram by Mr. G. F. Elliot, based upon specimens P. 40713–40715.
12. Coiled early stage of syntype, × 30. P. 40712.
13, 14. Diagrammatic drawings by Dr. F. R. S. Henson from specimens among the assemblage P. 40636–40645, × 20 approx.
15. Entire specimen, lateral view of syntype, × 30. P. 40711.
16. Syntype, broken off at intercameral neck to show internal fluting, × 40. P. 40710.

All the above specimens are from the Middle Eocene of Chadb, SW. Iraq.

FIGS. 10, 11. *Asterigerina rotula* (Kaufmann).

10. Section, in plane of coiling, × 40. P. 40709.
11. Transverse section, × 40. P. 40702.

Specimens from the Upper Eocene of Maaloula, near Damascus, Syria.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MIDDLE EAST FORAMINIFERA

PLATE 24

FIGS. 1, 2. *Asterigerina rotula* (Kaufmann) from Kirkuk, well 14.

1. Equatorial section showing traces of counter-septa, × 40. P. 40665 (ii).
2. Transverse section, × 40. P. 40665 (iii).

FIGS. 3–8. *Heterostegina* sp. cf. *Heterostegina ruida* Schwager, from Mushorah, well 1.

3. Transverse section, × 35. P. 40698.
4. Partial equatorial section, × 35. P. 40698.
5. Sub-equatorial section showing apertures connecting chamberlets of the same chamber, × 35. P. 40674.
6. Partial equatorial section showing apertures connecting adjacent chamberlets, × 35. P. 40699.
7. Transverse section, × 35. P. 40700.
8. Equatorial section of innermost whorl, × 35. P. 40674.

FIGS. 9–11. *Nummulites bouillei* de la Harpe, from Kirkuk, well 14.

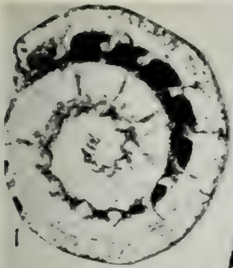
9. Partially decorticated specimen, × 15. P. 40671.
10. Mostly decorticated specimen, × 15. P. 40669.
11. Transverse section, × 20. P. 40673.

FIGS. 12–15. *Spiroclypeus anghiarensis* (Silvestri).

12. Equatorial section of specimen from Jebel Hafit, Oman, E. Arabia, × 20. In the same rock slice are *Eorupertia* sp., *Discocyclina* sp., *Baculogypsina* sp.
13. Transverse section of specimen from Kirkuk, well 78, × 20. P. 40683.
14. Transverse section of specimen from Jebel Hafit, Oman, E. Arabia, × 20. P. 40688.
15. Transverse section of specimen (perhaps microspheric) from Kirkuk, well 78, × 20. P. 40683.

FIG. 16. *Nummulites vascus* Joly & Leymerie var. *semiglobulus* (Doornink).

16. Transverse section, × 10. P. 40659.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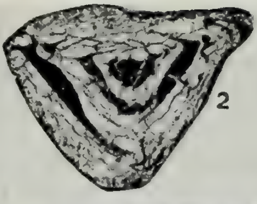
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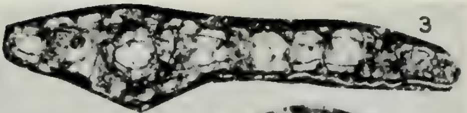
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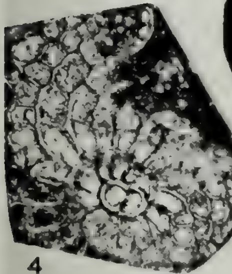
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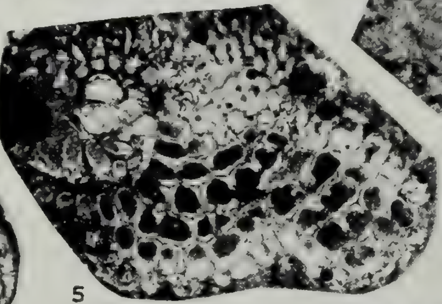
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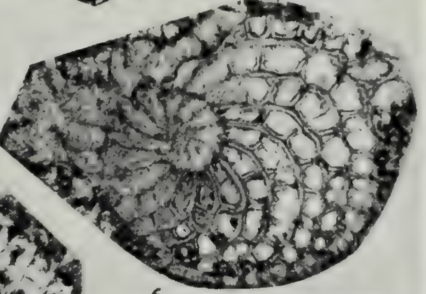
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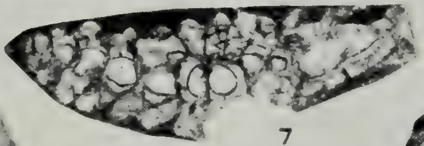
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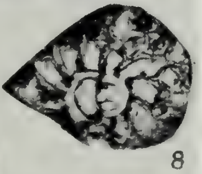
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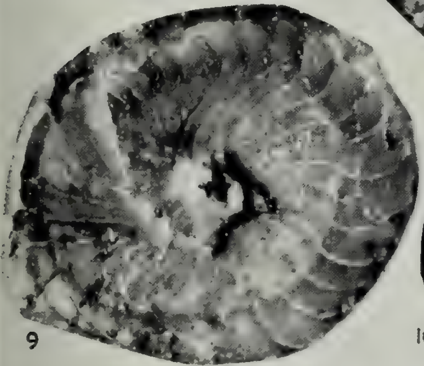
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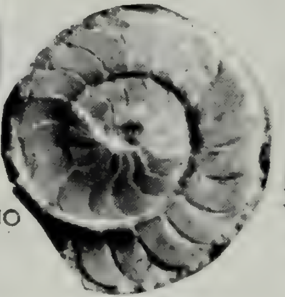
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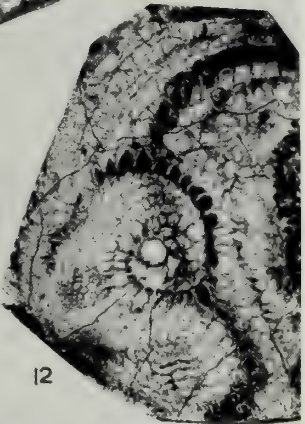
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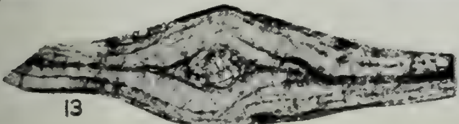
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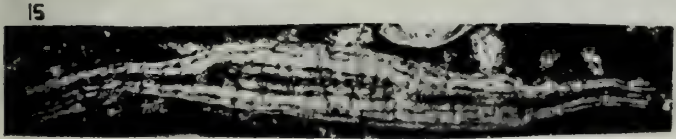
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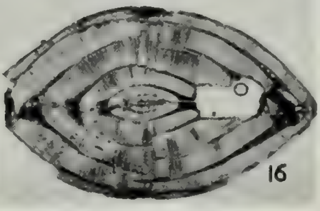
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MIDDLE EAST FORAMINIFERA

PLATE 25

Figs. 1, 2. *Nummulites vascus* Joly & Leymerie var. *semiglobulus* (Doornink).

1. Transverse section of specimen from Kirkuk, well 31, × 10. P. 40660.
2. Approximately equatorial section of specimen from Kirkuk, well 31, × 10. P. 40661.

Figs. 3–9. *Nummulites perforatus* (de Montfort) var.

3–5, 9. Megalospheric form of variant described and figured by Checchia-Rispoli (1911) as *N. bayhariensis*, × 11.

3. Transverse section of specimen from Kirkuk, well 14. P. 40665 (i).

4, 5. External views of specimens from Kirkuk, well 42. P. 40655–40656.

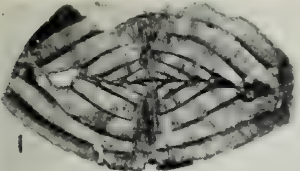
9. Equatorial section of specimen from Kirkuk, well 43. P. 40650.

6–8. Microspheric form, '*Nummulites perforata* d'Orbigny var. *uranensis* de la Harpe'.

6. Transverse section, off centre, of specimen from Kirkuk, well 43, × 5. P. 40676.

7. External view of specimen from Kirkuk, well 42, showing the vorticiform curvature of the septal filaments, × 4. P. 40666.

8. Equatorial section of specimen from Kirkuk, well 42, × 5. P. 40670.



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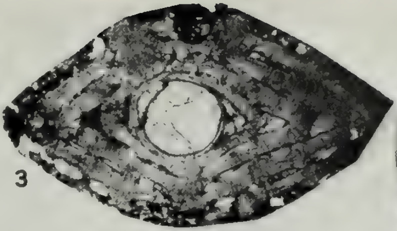

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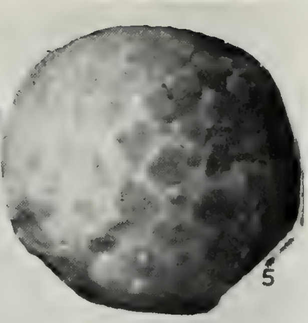

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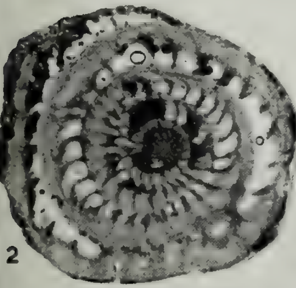

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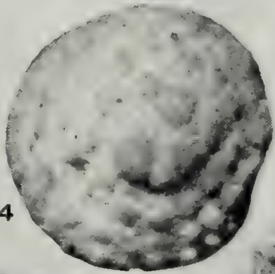

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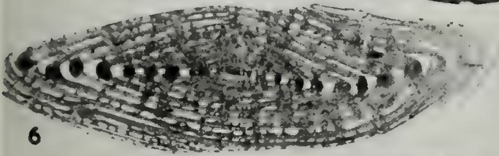

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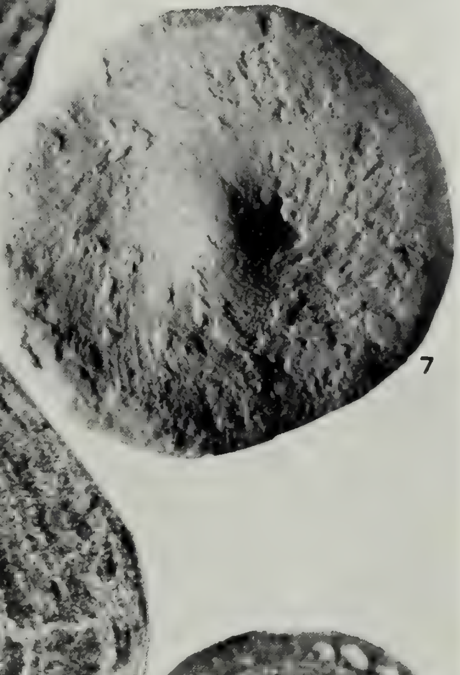

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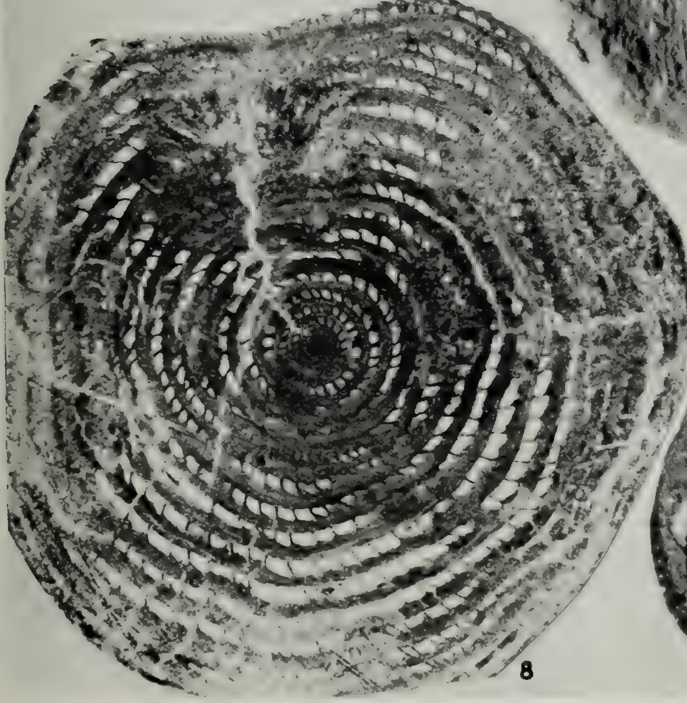

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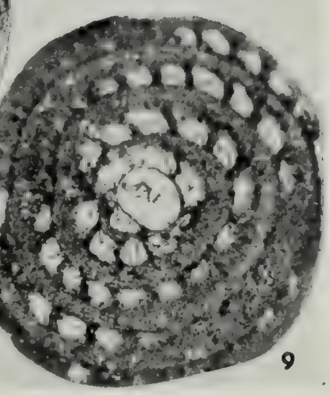

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MIDDLE EAST FORAMINIFERA

BRITISH MUSEUM NATURAL HISTORY
PRESENTED
2 2 MAY 1952

PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

NATURAL HISTORY
PRESENTED
22 SEP 1952

AUSTRALIAN ARTHRODIRES

ERROL WHITE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 1 No. 9
LONDON: 1952

AUSTRALIAN ARTHRODIRES

BY

ERROL WHITE

BRITISH MUSEUM NATURAL HISTORY

Pp. 249–304; *Pls.* 26–31; 41 *Text-figures*

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LONDON: 1952

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in 1949, is issued in five series, corresponding to the Departments of the Museum.*

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This paper is Vol. 1, No. 9 of the Geological series.

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued September, 1952 *Price Fifteen shillings*

AUSTRALIAN ARTHRODIRES

By ERROL WHITE

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SYNOPSIS

A small collection of arthrodire remains is described from the Middle Devonian strata in the Burrinjuck Dam area, New South Wales. Three, possibly four genera are represented, two of them new, and a third, congeneric with Hills's '*Coccosteus osseus*', shows part of the neurocranium: this form is considered to be a brachythoracid. A note is added on *Notopetalichthys*, from the same beds. The bearing of this new evidence on existing theories on the development of arthrodire fins and armour and on the classification of the group is discussed and tentative new hypotheses are put forward.

I. INTRODUCTION

In 1939, just before the war, Mr. R. Bedford, Director of the Kyancutta Museum, South Australia, sent to the British Museum for identification five specimens showing the remains of fishes that Mr. W. E. Williams, of Cootamundra, New South Wales, had collected from the Middle Devonian marine limestones of the Burrinjuck Dam area, New South Wales, some 35 miles north-west of the federal capital, Canberra.

Owing to the war and subsequent dislocation caused by the evacuation of part of the collections and damage to the Museum, it was not until ten years later that I was able to take up the study of the specimens seriously. Although for the most part fragmentary, they were extraordinarily well preserved and bid fair to show structures rarely seen in these animals. The external features had been freed from the dark grey limestone matrix with much patient skill by Mr. Bedford, but it was decided to employ the acetic acid process (Toombs, 1948) in an effort to expose some of the delicate inner structures that appeared to be present in section on the fractured surfaces. Owing to the cracked state as well as the natural delicacy of the bones the process proved to be a very long and tedious one, for only a small portion could be exposed to the acid at a time, and had then to be covered with a protective coat of cellulose while a neighbouring area was treated. Altogether the work, done at intervals, took well over a year, but was most skilfully carried out by Mr. H. A. Toombs.

The specimens eventually proved to be even more interesting and important than was at first supposed, and their discovery reflects great credit on their collector, Mr. W. E. Williams, with whom Mr. Bedford kindly put me in touch. Mr. Williams has now most generously presented them to the British Museum (Natural History) and has given me full information concerning the localities. The specimens are preserved in dark grey limestones from the Murrumbidgee Series, of Couvinian (lower Middle Devonian) age (Hills, 1941: 46), from two localities: (1) Taemas, on the Murrumbidgee River, where Süssmilch found the head of *Dipnorhynchus* [*Ganorhynchus*] *süssmilchi* (Eth.); and (2) Barber's, about 10 miles to the west-south-west on the Goodradigbee River.

The five specimens are all of arthrodires, representing at least four genera, of which two are doubtless new. They comprise:

1. The greater part of the body-armour of a new arctolepid from Barber's.
2. An isolated brachythoracid gnathal plate from Barber's.
3. A slice of the head of a species related to the Victorian '*Coccosteus osseus*', from Taemas.
4. A fragment of a median dorsal plate, apparently of the same form as (3), from Taemas.
5. The complete paranuchal plate of a large new brachythoracid, from Taemas.

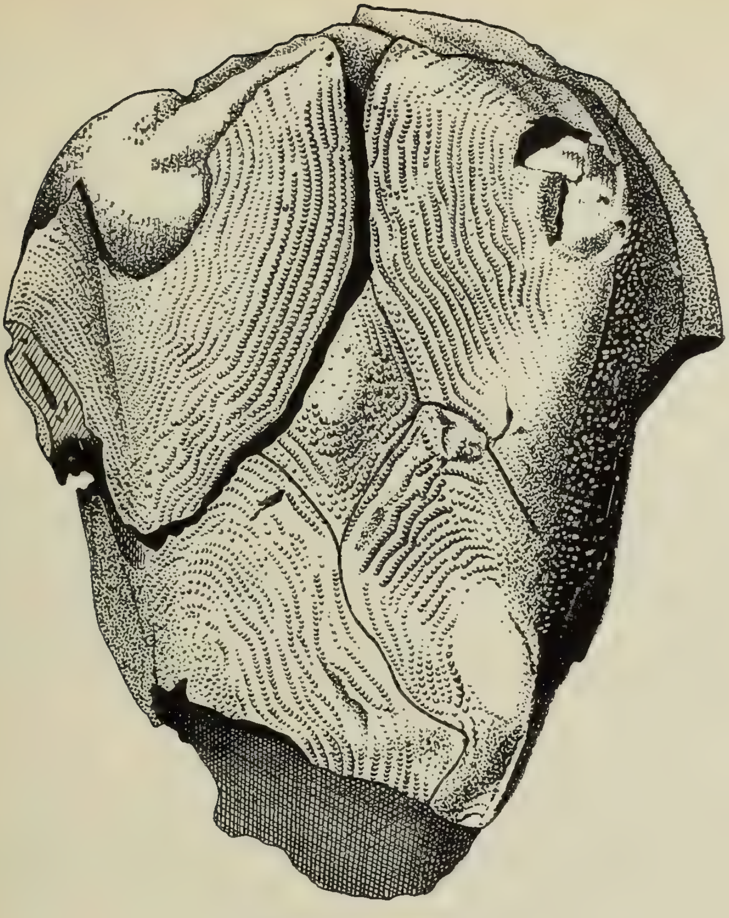
These then represent three, possibly four, diverse genera of arthrodires, and if we add the *Dipnorhynchus* and the petalichthyid, *Notopetalichthys*, from 'Goodra Vale' (Woodward, 1941—further note below), we have a total of five or six genera of fishes from seven specimens, and it is obvious that in the Burrinjuck area there is to be found a fish-fauna of outstanding importance among those in Devonian strata.

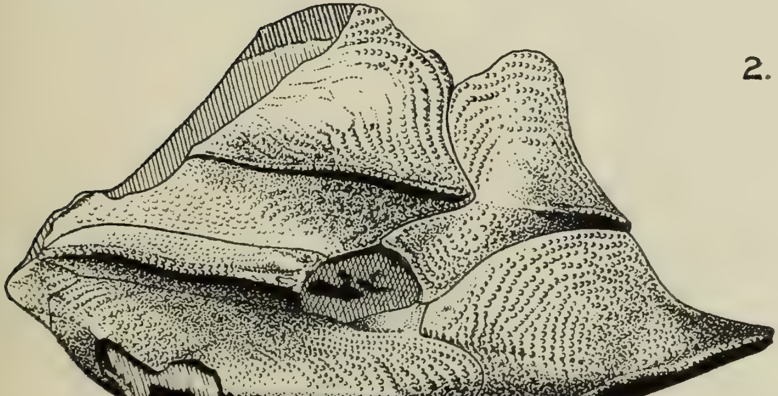
II. SYSTEMATIC DESCRIPTION

Order *ARCTOLEPIFORMES* (see p. 298)

Sub-order ARCTOLEPIDI

The most characteristic features of the arctolepid body-armour are the full development of the plates to cover all but the caudal region (with, I believe, the formation of a restricted pectoral fenestra) and hitherto the development of large pectoral spines. In the genus next described this last feature is absent, but there can be no





Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIG. 1. Body-armour, in ventral view. The holotype, P.27073, × 1½.

TEXT-FIG. 2. The same specimen, left side with right AVL removed, × 1½.

doubt it must be included in this order, for the body-armour is otherwise quite typical.

It is also evident that the compass of the sub-order will have to be enlarged to include the more obvious derivative groups, such as the acanthothoracans which, unlike the ptyctodonts and phyllolepids, are not sufficiently specialized to warrant being considered as independent sub-orders.

Super-family WILLIAMSOSTEI

DIAGNOSIS. Arctolepids with the principal characters of the only family, the Williamsaspidae.

Family WILLIAMSASPIDAE

DIAGNOSIS. Arctolepids with rounded undersurface and spinal plate placed accordingly high on side without development of lateral spine. Lateral plates tall, the anterior with a broad mesial flange or apron at right angles to its lateral surface; the posterior, elbow-shaped with the lower anterior shank forming posterior dorsal margin of pectoral fenestra. Scapulo-coracoid cartilage completely invested with perichondrial bone, without scapular or lateral processes, reaching from posterior margin of pectoral fenestra to near midline in front, the coracoid processes being separated apparently by the thickness of the mesial surfaces of the interlateral plates.

Only one genus known.

Genus ***WILLIAMSASPIS*** nov.

DIAGNOSIS. As for family (only genus).

The genus is named in honour of Mr. W. E. Williams of Cootamundra, N.S.W., who collected this and the other new specimens described and generously presented them to the British Museum; the species in honour of Mr. R. Bedford of the Kyancutta Museum, S. Australia, who first developed the specimen and through whose interest the specimens came to the British Museum.

SPECIES. The genotype only.

Williamsaspis bedfordi sp. nov.

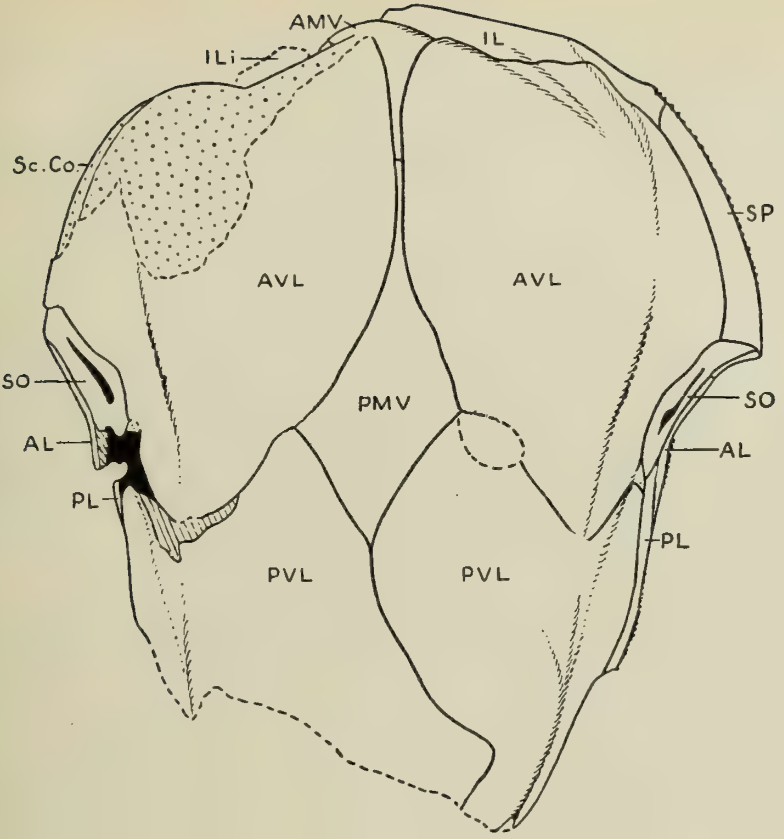
(PLS. 26–29; TEXT-FIGS. 1–18, 38, 39E)

DIAGNOSIS. As for family and genus (only species).

MATERIAL. The unique holotype, comprising the lower two-thirds of the body-armour (P.27073).

FORMATION AND LOCALITY. Middle Devonian; Barber's, Goodradigbee River, N.S.W.

DESCRIPTION OF SPECIMEN. This remarkable specimen (Pls. 26, 27; Text-figs. 1, 2) consists of the body-armour less the dorsal and dorsolateral plates. The anterior and posterior lateral, spinal, interlateral, anterior and posterior ventral plates of the left side, the anterior and posterior median ventral plates, and the imperfect posterior lateral and ventrolateral plates of the right side are all firmly in position; but the plates of the right fore-quarter, comprising the anterior lateral and ventrolateral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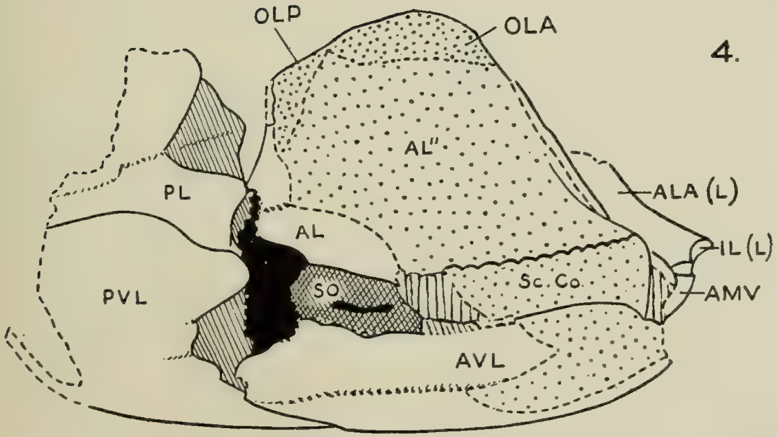
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PVL
AVL

4.

Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIG. 3. Outline of body-armour in ventral view. The holotype, P.27073, × $1\frac{1}{2}$.

TEXT-FIG. 4. The same specimen, right side, slightly uptilted, × $1\frac{1}{2}$ approx.

(For explanation of lettering see pp. 303–304.)

plates, the interlateral and spinal with the fin-socket, have slipped as one piece a little downwards, forwards, and inwards, leaving a small gap between the side plates and forcing the right anterior ventrolaterals over the median plates.

The median bones and those of the left side are almost complete except for the central parts of the anterior lateral and ventrolateral and the tip of the posterior ventrolateral. Of the right plates (Text-figs. 4, 6) the whole of the spinal and all but a fragment of the interlaterals have been lost, leaving the impression of the mesial face of the scapulo-coracoid cartilage and fragments of perichondrial bone; while practically the whole of the anterior lateral is now preserved as an internal impression, and the front of the anterior ventrolateral, the hinder margin of the posterior lateral, and nearly half the posterior ventrolateral are missing. Nevertheless these are mechanical defects, the actual preservation of the bones being extremely fine. The specimen was very well developed by Mr. R. Bedford, to whom Mr. Williams, the discoverer, sent it, and was finished off in the British Museum (Natural History) by Mr. H. A. Toombs with the acetic acid treatment. The very finest details are now to be seen, some of the smaller plates being largely free of the matrix on the inside as well as the outside. It will be convenient to describe the specimen upside down, beginning with the ventral surface, which is virtually complete.

The length as preserved (and there are only a few millimetres missing from the posterior ventrolateral plates) is 7·2 cm., the maximum breadth, based on double the complete left side at the level of the tip of the spinal plate, is approximately 6·5 cm.

The median ventral plates (Pl. 26, fig. 1; Pl. 28, fig. 3; Text-figs. 3, 10) are large and in contact with one another, like those in *Coccosteus* (Heintz, 1938*a*: text-figs. 1, 7) and certain arctolepids such as *Euryaspis*, the anterior (AMV) being shaped like an axe-head with a rounded anterior margin fitted behind the interlateral plates at their junction, while the posterior plate (PMV) is diamond-shaped with the prolonged front angle truncated. Both plates are gently convex and the marginal contacts are presumably normal, i.e. they are overlapped by the ventrolateral plates on all sides, except where they are in contact with one another.

The anterior ventrolateral plates (Pl. 26; Pl. 28, fig. 3; AVL, Text-figs. 3, 6, 7, 10) are remarkably tumid, or shell-like, and form a substantial part of the lateral wall with a very distinct lateral keel running backwards well above base level from the apex, which is presumably the growth centre, while two or three shallow grooves run forwards and inwards on to the interlateral. In front view (Text-figs. 6, 8) the basal part below the keel is convex, so convex that the anterior median ventral plate lies in a wide groove, whereas above the keel the lateral part is concave; but to the rear both curves become less pronounced (Text-fig. 12). Longitudinally the long basal portion behind the apex is gently convex, and again the short anterior part, which rises to the interlaterals, is concave.

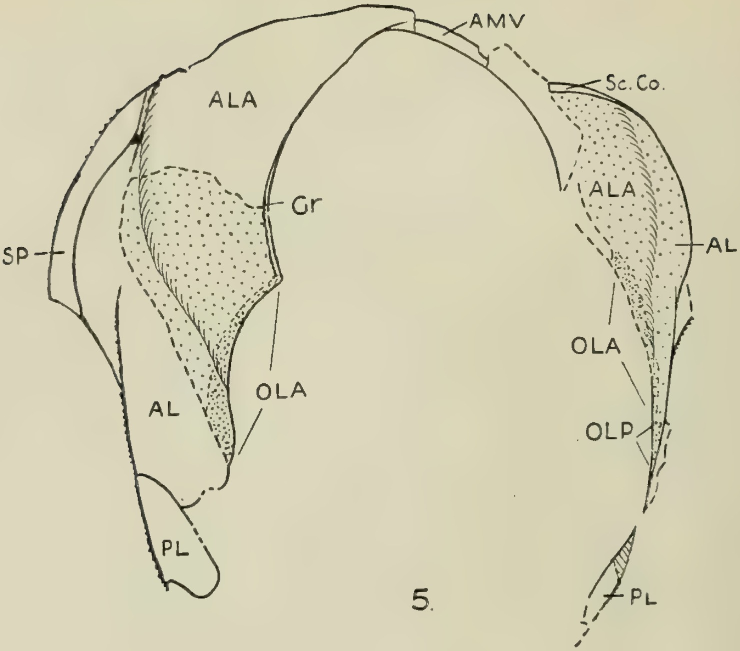
The right anterior ventrolateral plate has slipped inwards slightly and shows by its entire margins that it overlapped the two median ventral plates and the front of the posterior ventrolateral: the left plate has the same form, apart from a slight healed injury near the PMV–PVL contact. The contact in front with the interlateral and with the spinal along the top (both presumably being sutured to or slightly overlapped by it) is very close, for they have moved as one piece with the anterior ventrolateral and the anterior lateral. In side view (Text-figs. 2, 7) the margin with the spinal is almost straight and continues straight behind it under the pectoral fenestra for half its length, and then turns sharply upwards to form a small triangular projection to meet the posterior lateral, closing the fenestra and cutting off the posterior ventrolateral from the margin.

The posterior ventrolaterals (Pl. 26; Pl. 27, fig. 2; PVL, Text-figs. 3, 4, 7, 10) are very dissimilar in shape ventrally, for the right plate widely and irregularly overlaps the left instead of, as seem more usual, the left moderately and regularly overlapping the right. In side view the ventral face of each plate at first continues the curve of the anterior plate, so that the general longitudinal basal profile is markedly convex. The main ventrolateral keel is very faint in front of the centre of the plate, so that the plate is at first rounded in cross-section, but thereafter the keel is strongly developed with a complementary groove over it, sharply dividing the side from the undersurface, both of which become flattened and lie almost at right angles to one another. The anterior margin of each plate is strongly embayed by the overlap of the plate in front, but at the top of the indentation the margin turns at right angles to run vertically for a short distance against the anterior ventrolateral prominence. The dorsal margin, in contact apparently by suture with the posterior lateral, is sigmoidal, being at first slightly concave and then broadly convex as far as the hinder margin which it meets at a wide angle. The free hinder margin sweeps down and backwards in a deep hollow curve to meet the ventrolateral keel at a very acute angle, so that the length of the plate dorsally is only about two-thirds or less of its maximum (ventral) length.

The interlateral plates (Pls. 26, 27; Pl. 28, fig. 3; IL, Text-figs, 3, 4, 6–8, 10) apparently face wholly forwards and downwards, for above they seem to be sutured to the apron of the anterior laterals along the front edge of the armour, forming a very prominent denticulated keel, largely abraded in this specimen, passing into that of the spinal. They meet one another in the midline along a minute vertical facet, and below they are firmly attached for a short distance to the anterior median ventral (where they are narrowed by the convex front margin of that plate) and to the anterior ventrolateral as far as the rounded anterior lateral corner where each side is closely sutured to the corresponding spinal plate.

The spinals (Pl. 26; Pl. 27, fig. 1; Pl. 28, fig. 3; SP, Text-figs. 3, 5–10, 13*a*), forming the main lateral keels, curve gently backwards to the pectoral socket of which they form the anterior, partly transverse margin, but without formation of a spine. These plates are bluntly triangular in section (Text-fig. 13*a*) since, unlike the interlaterals, they have a large, gently convex upper surface which meets the lower edge of the anterior laterals at a wide concave angle.

The anterior lateral plates are very remarkable (Pl. 26, fig. 2; Pl. 27; Pl. 28, figs, 1, 3; AL, ALA, Text-figs. 3–10). High and wide with a strong keel about a third of the way up the side, they have an extremely broad mesial lamina or apron (ALA) in front at right-angles to the lateral face. The apron, which has a peculiar ornamentation of its own (see p. 265), slopes in a gentle hollow curve upwards and backwards very nearly at 45° to the line of the spinal plate. Transversely it was also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AL
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OLA
OLP
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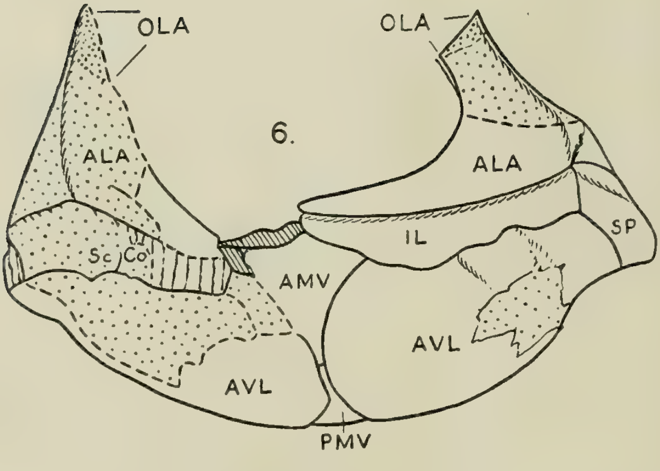
PL

5.


OLA
OLA
ALA
ALA
Sc
Co
IL
SP
AMV
AVL
AVL
PMV

6.

Williamsaspis bedfordi gen. et sp. nov.

Text-fig. 5. Outline of body-armour in antero-dorsal view. The holotype, P.27073, × 1½ approx.

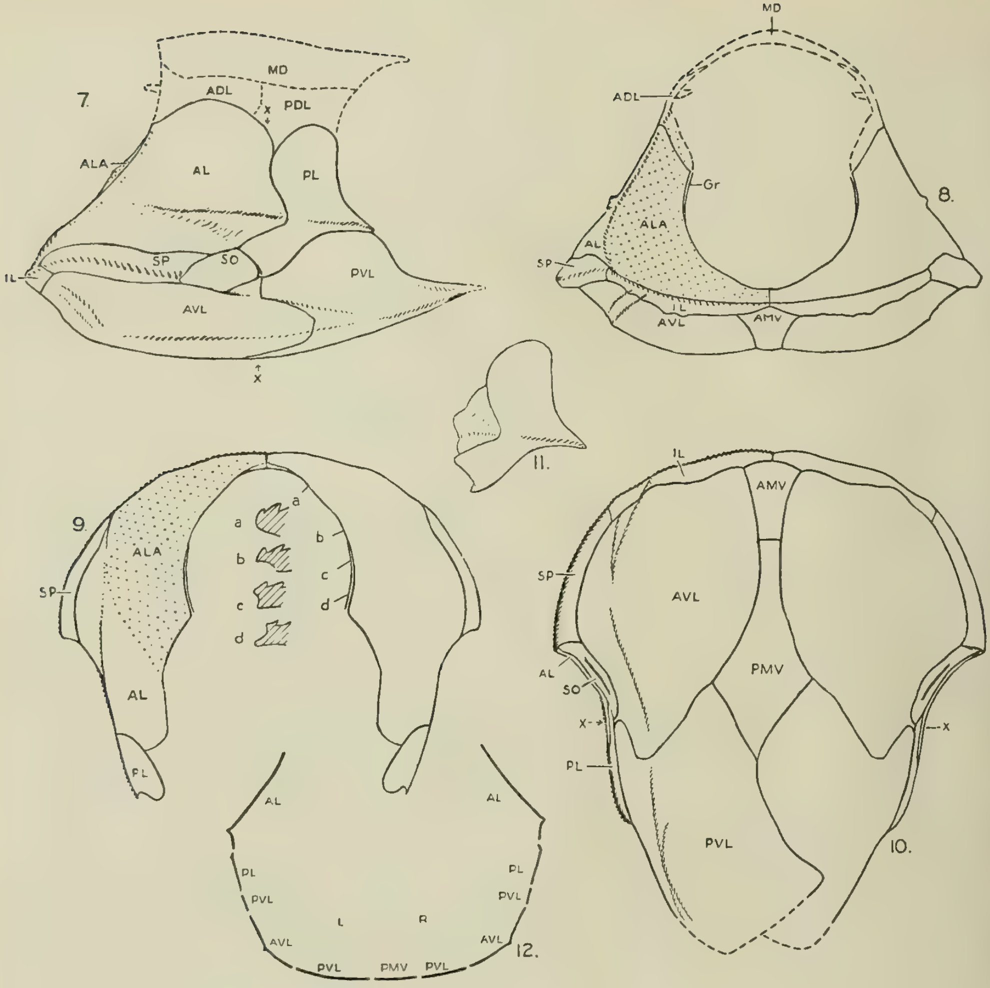
Text-fig. 6. The same, front view, slightly uptilted, × 1½ approx. Shading &c. as in Text-fig. 4.

(For explanation of lettering see pp. 303–304.)

slightly concave. The mesial margin is deeply embayed, forming almost the quadrant of a circle, but is at the same time slightly sinuous. The free edge is smoothly rounded upwards in the lower half, but about half-way a groove (Pl. 28, fig. 1; Gr, Text-figs. 5, 8, 9) comes from the undersurface on to the free edge itself, finally facing partly upwards along the margin. As noted above, the division between the apron and the interlateral plate seems to be along the line of the ridge, continuing the suture between the lateral face and the spinal, but no suture can be detected externally and only a suggestion of such internally in broken cross-sections, the two plates being fused together. The angle between the apron and the lateral face (AL) of the anterior lateral is virtually a right angle, rounded off on the inner surface shown on the internal cast, but the bone itself is only preserved at the lower front end where a sharp ridge dividing the two surfaces is actually present and may continue to the top. The lateral face is roughly trapezoidal, except for a large triangular posterior process bearing the keel and overlapping the posterior lateral, for the rounded top margin is shortened by the slope of the apron and the lower margin cut off by the pectoral opening.

The posterior laterals are equally curious in form, being elbow-shaped (Pl. 26, fig. 2; Pl. 27, fig. 2; PL, Text-figs. 4, 7). Each has a narrow lower shank running steeply below the anterior lateral process down to the pectoral opening, of which it forms the concave posterodorsal border, and a wider upper shank with a rounded dorsal border passing into a gently concave free posterior margin. The latter slopes backwards and downwards, forming a very acute angle with the sigmoid lower margin, which in front has a very small contact with the triangular process of the anterior ventrolateral. The keel of the anterior lateral plate is continued, at first faintly (in part due to abrasion) and then strongly to the point of the posterior angle. The curious external shape of this plate is due to the strong triangular overlap of the anterior lateral, but even when isolated it is still very irregular in outline (Text-fig. 11) with its fan-shaped overlapped area.

All the dorsolateral plates and the median dorsal had become loosened and disappeared before fossilization, but we know a little about both the anterior and posterior dorsolaterals from the extent of the overlapping areas on the anterior lateral (OLA, OLP, Text-figs. 4–6). The area overlapping the anterior dorsolateral runs forwards along two-thirds of the upper lateral margin of the anterior lateral plate, continuing as a narrow and decreasing selvage to the mesial margin of the apron, so that the anterior dorsolaterals also had a transverse flange that formed the top of the apron. The extent of the posterior dorsolateral is not so certain, but presumably its hinder margin continued the curve of the posterior lateral. A possible restoration of the missing plates is given in Text-figs. 7, 8. If the anterior dorsolateral plate bore an articular peg, as it does in most arthrodires, and not just an overlapped flange, such as Stensiö (1944: text-figs. 17*a*; 1945: 7) records in *Kujdanowiaspis*, the median dorsal plate must have been at least as high as shown to allow for the depth of the skull, since the median articulations at the base of the skull must, of course, be in line with the external pair on the armour to allow the head to swing. But in view of the rapid narrowing of the armour upwards, both laterally and transversely, the level of the back was probably not much higher. If the restoration is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Williamsaspis bedfordi gen. et sp. nov.

Text-figs. 7–10. Restorations in outline of body-armour: (Fig. 7) direct side view; (Fig. 8) front view, tilted slightly forwards; (Fig. 9) in antero-dorsal view, at right angles to the apron, with cross-sections of free inner edge (*a–d*); and (Fig. 10) ventral view. The left sides of Figs. 8–10 show the ridges, the right sides outlines only. Area of anterior lateral apron stippled. Approx. nat. size.

Text-fig. 11. Restoration in outline of left posterior lateral plate showing area overlapped by anterior lateral plate. Approx. nat. size.

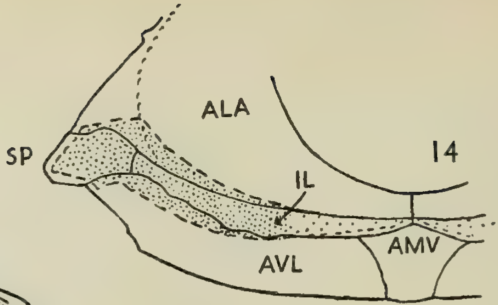
Text-fig. 12. Cross-profile at *X–X* in Figs. 7 and 10.

(For explanation of lettering see pp. 303–304.)

approximately correct, then the relatively high position of the hinges does give, subject to the limiting factor of the size of the gap between the nuchal and median dorsal plates, a wide arc of possible movement to the head which would require an extremely flexible throat. It also means a relatively large branchial chamber, and where this feature is marked, as in the 'monaspids' (Heintz, 1929: text-fig. 9), the ptyctodonts (Watson, 1938: text-fig. 3), *Williamsaspis*, and rather less so in *Palaeacanthaspis* (Stensiö, 1944: text-fig. 3), the anterior lateral apron is also conspicuous. To that extent there is some correlation between these two features, but they are not proportionately developed.

The form of the scapulo-coracoid can be accurately determined from the complete interlateral and spinal plates of the left side and the impression of the girdle on the internal cast shown on the fractured right side (Pl. 27; Pl. 28, fig. 3; Sc Co, Text-figs. 3–6, 13–15, 17, 18), where in places part of the relatively thick perichondrial bone with which it was invested is preserved. Seen from above or below it is very similar in form to that shown in Stensiö's (1944: text-fig. 17B) restoration of *Kujdanowiaspis* and is presumably that of a typical arctolepid (Text-fig. 13). The scapulo-coracoid runs from the front midline, where the coracoid process is separated from its fellow only by the minute median wall of the containing interlateral, backwards in a gentle curve to the hinder edge of the pectoral socket behind. It widens steadily from the midline of the body to about two-thirds of the distance to the anterior lateral corner and then narrows sharply, forming a distinct inner angle, the anterior mesian angle (AMA, Text-fig. 13). After passing laterally under the spinal plate it gently widens again to the front of the socket where it forms a slightly obtuse external angle but no spine, and behind which it forms a wedge, with a long concave posterolateral outer face fitting the pectoral socket. In cross-section (Text-fig. 13*a*) the cartilage is roughly triangular, following the shape of the spinal keel, with the inner surface mostly convex, but slightly sinuous and facing somewhat upwards. The outer surfaces meet at an angle of about 60°, the lower being nearly horizontal. The perichondrial bone is preserved in a number of places and evidently invested the whole cartilage and lined the foramina in it. It is fused along the outer faces with the investing dermal bones; in front it has only the apron above and the interlateral and the anterior ventrolateral below, but along the sides the spinal covers the whole of both external surfaces, with only narrow selvages under the anterior lateral above and the anterior ventrolateral below.

In front view (Pl. 28, fig. 3; Text-figs. 6, 14, 18) the coracoid process seems to have tapered mesially (distally), although this part is not preserved in the fractured right side, but its shape can be roughly determined from the form of the enveloping interlateral on the left side. It increases gradually in depth towards the sides, rising steadily as it approaches the spinal margin, where it immediately straightens out and passes levelly under the spinal plate as far as the pectoral fenestra. There it turns up to fit under the socket, wedging out at the margins, so that the form of the socket face is preserved by the perichondrial bone layer. The lateral, scapular part of the cartilage is of even depth (Pl. 27, fig. 2; Text-figs. 4, 15, 17) with no scapular process, but the whole impression of the upper margin on the anterior lateral is pinked where the dorsal neurovascular canals passed over the upper edge of the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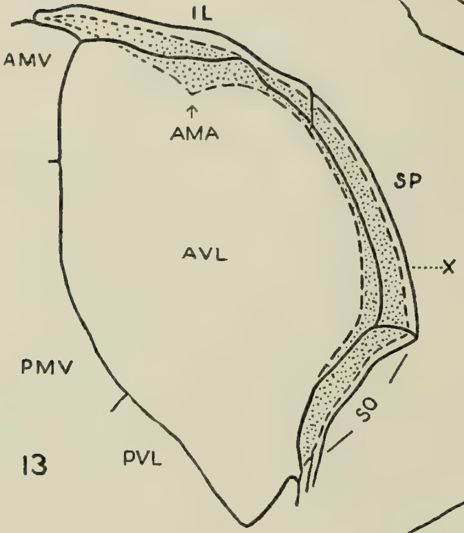
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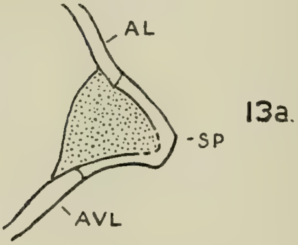
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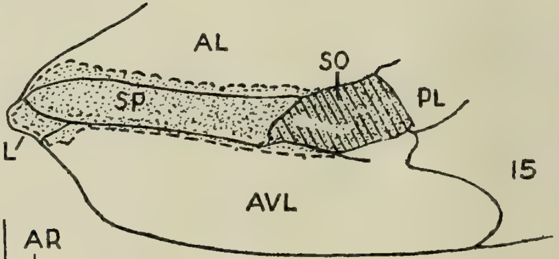
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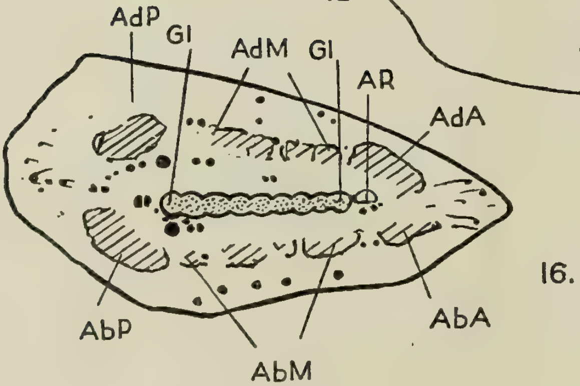
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TEXT-FIGS. 13–15. Restorations in outline of the forequarter of carapace to show form of the scapulo-coracoid (stippled with pectoral fenestra shaded): (Fig. 13) from below with (13*a*) enlarged cross-section at *X*; (Fig. 14) from the front; (Fig. 15) from the side. × 1½ approx.

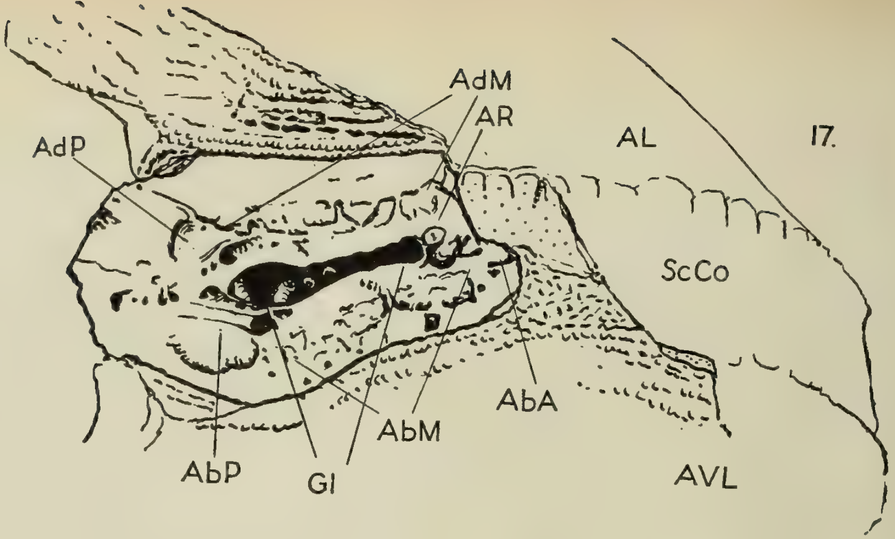
TEXT-FIG. 16. Restoration in outline of right pectoral fenestra flattened out. Cartilage stippled; muscle attachment-areas diagonally shaded; neuro-vascular foramina black. × 4½ approx.

(For explanation of lettering see pp. 303–304.)

scapulo-coracoid and down the dorsolateral outer face. There are indications of over twenty of the dorsal vessels from a little in front of the fin-socket as far forward and mesially as the right side is preserved, i.e. about two-thirds of the way along the interlateral border. The notches are not absolutely regularly disposed: in front (Text-fig. 18) the notching is much deeper and more oblique, the canals forming strong ridges on the perichondrial layer of the mesial face which finally overlap the ventral series; behind, near the fin-socket, one or two of both dorsal and ventral series actually passed through the cartilage itself as the bony tubes show, instead of between the dermal basal layer and the perichondrial layer. The passage of the ventral series is not so clearly marked as the upper, these canals passing under the cartilage without deeply notching it.

The exposed surface of the scapulo-coracoid is completely surrounded by plates forming a conspicuous pectoral fenestra (Pl. 26, fig. 2; Pl. 27, fig. 2; Pl. 29; SO, Text-figs. 3, 4, 7, 10, 15–17, 19). It is bordered by the spinal plate in front, the laterals above and behind, and the anterior ventrolateral alone below, for this last plate sends up a small triangular projection to meet the posterior lateral and so completely excludes the posterior ventrolateral plate from the fenestral margin. It measures approximately 1·5 cm. in length when flattened, or about two-ninths of the maximum length of the body-armour, but appears to be much shorter owing to its concave face and partly diagonal position (Pl. 26, fig. 2). The face is not vertical but directed slightly downwards (Pl. 26, fig. 1; Text-fig. 10). In outline (Text-fig. 16) it forms a rough unequal-sided pentagon with a long dorsal margin sloping downwards, so that it is more pointed and shallower in front than behind. The surface is completely covered with a thin layer of perichondrial bone except for the actual articular surface of the basals, which was unossified (Text-fig. 16, Gl–Gl). The bone is, of course, continuous with the similar bone encasing the rest of the scapulo-coracoid cartilage which is fused with the basal layers of the neighbouring dermal bones except apparently that of the posterior lateral behind where, owing to the fine wedging out of the contained scapular cartilage, the outer perichondrial lamina meets the inner in a free knife-edge. On the right side where all the anterior plates have become slightly detached, the fenestral cover has moved as one piece with them and shows an unbroken dorso-posterior margin (Pl. 29, fig. 1; Text-fig. 17). The most conspicuous feature of the exposed surface is the long slit which in life was occupied by the cartilaginous articular surface of the pectoral basals. Only on the right side (Pl. 29, fig. 1) is part of the actual edge of the bone surrounding the articular area preserved, along the front half of the upper margin and the anterior end. The margin is slightly raised so that the articular surface was in the form of a low narrow ridge, and from the five faint more or less equal crenulations preserved we may estimate that there were some nine separate basals. Immediately in front, isolated but in contact, is a much narrower bony cup (AR, Text-figs. 16, 17) which may be for the direct attachment of the anterior and perhaps spinous, fin-ray. It has a faint median vertical ridge.

The muscle-scars are very clearly shown and are remarkably symmetrical about the articular ridge. On each side the musculature was divided into three parts—a wide shallow depression in front, a median series of roughened areas cut up by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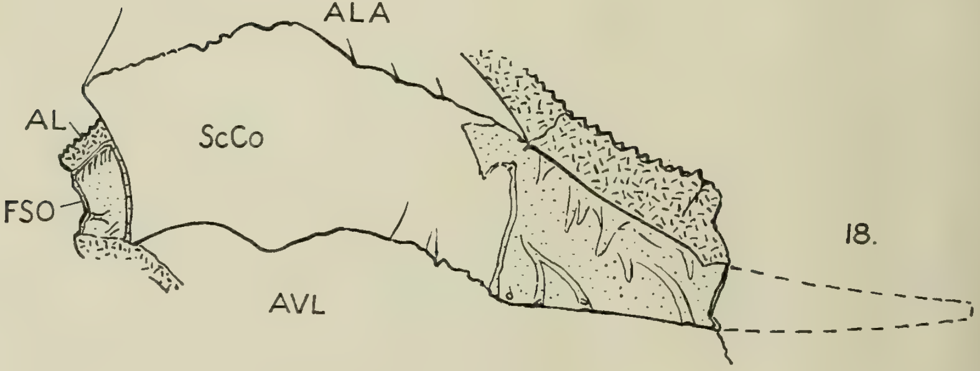
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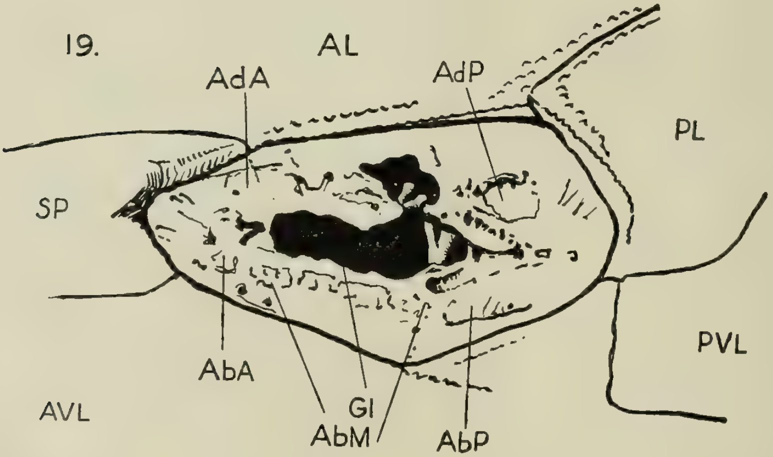
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TEXT-FIG. 17. Right pectoral socket and internal impression of scapulo-coracoid in side view, *cf.* Pl. 29, fig. 1. The holotype, P.27073, ×4½.

TEXT-FIG. 18. Front view of right scapulo-coracoid of same specimen showing either the internal impression (plain) or the medial perichondrial cartilage (dotted). Broken surfaces of plates are long stippled. *Cf.* Pl. 28, fig. 2. ×3½ approx.

TEXT-FIG. 19. Left pectoral socket of same specimen, *cf.* Pl. 29, fig. 2. ×4½.

(For explanation of lettering see pp. 303–304.)

vascular grooves, and still wider shallow areas behind, the only marked difference between the adductor (dorsal) series and the abductor (ventral) series being that the dorsal posterior and the ventral anterior areas are somewhat smaller than their opposites.

In this fish all the vessels and nerves supplying the fin must, of course, come through the girdle and pass out through the limited surface of the pectoral fenestra. Apart perhaps from some of the finest when filled with matrix, the foramina are easily recognized in the perichondrial bone (Pl. 29, Text-figs. 16, 17, 19) and the ossified tubes of some of the larger vessels may be seen through the articular slit, especially on the left side where the margins are most extensively broken. It is not possible to assign to these irregularly distributed foramina their precise functions, but the important vessels are concentrated largely at the hinder end of the articular ridge—one particularly large and one double foramen below, a double foramen behind, and a very large opening above. These doubtless carried the nerves of the brachial plexus and branches of the subclavian artery and vein to both dorsal and ventral sides of the fin. The small foramina provided passage for the dorsal and ventral branches of the cutaneous arteries, veins, and nerves, and almost all lie at the end of grooves directed towards the articular ridge.

The ornamentation of the plates consists for the most part of well-separated lines of closely packed stellate tubercles (Pls. 26–29; Text-figs. 1, 2) disposed roughly parallel with the margins of the plates, and is rather like that on certain plates, such as the anterior lateral, of *Phlyctaenaspis*, except that the lines are finer and the tubercles (Pl. 28, fig. 2) more coarsely stellate. The valleys between are finely crinkled and owing to the thinness of the external layer the tubules of the spongiosa are frequently seen. Near the centre of the larger plates the tubercles are more irregularly disposed and on the longitudinal ridges or keels closely massed, especially on the spinal-interlateral keel where they are slightly, but only slightly, enlarged. The only exception to this type of ornamentation is on the apron of the anterior lateral plate which is covered with sharply pointed, depressed triangular pyramids (Pl. 27, fig. 1; Pl. 28, fig. 1). These are directed forwards or antero-laterally with the large, flat upper face showing as a rule three ridges, one median and one along each side, meeting at the apex of the triangle. How clearly the ornamentation of the apron was marked off from that of the side is not certain, as the bone of the angle between is lost except at the very front bottom corner, and here they are separated by a ridge.

One interesting point about the ornamentation of the apron in this particular specimen is that along the lower outer margin near the angle between the two faces an area has been cleared of its original coarse ornament and this has later been replaced by a few scattered and very small tubercles of the same design as the larger originals. Whether this defect is due to accident or disease is not certain, but the final result is very like that of the obvious bites seen on the skull-roof of another genus (see p. 271 *infra*).

REMARKS. *Williamsaspis* presents a number of peculiar features which isolate it systematically. Its well-developed armour with the large spinal plate show its arctolepid affinities, but so far as I know it is the only arthrodire with a well-rounded undersurface and the spinal plate consequently placed well up the side. *Euryaspis*, it is true (Bryant, 1934: 139), has the anterior ventrolateral plates 'arched very gently from side to side in front', but it has a conspicuous lateral spine, while in the very different *Palaeacanthaspis* (Stensiö, 1944: text-figs. 3, 4) the same plates form a small part of the lateral surface but the much reduced ventral armour is flat and there again a lateral spine is present. Except for the laterally compressed genera from Wildungen (Oxyosteidae, Synaucheniidae, Gross, 1932:39, text-figs. 17–25), arthrodires seem to have had flat bottoms. But it is the undeveloped condition of the lateral spine on the large spinal plate that is so characteristic of *Williamsaspis* and with it goes the evidence of well-developed pectoral fins provided by the pectoral fenestra and the seating of the fins. The absence of a large pectoral spine is, I think, also an unspecialized character, due to non-development rather than loss. But the curious elbow-shaped posterior lateral plates, which forms a large arc of the margin of the pectoral fenestra, is a more original development, so far unknown in other arthrodire genera, while the extreme development of the apron of the anterior lateral plate still further sets it apart from other arctolepids.

By and large it seems most appropriate to treat *Williamsaspis* as the only member of a special group of arctolepids, characterized by the undeveloped pectoral spine, its peculiar pectoral fin, large apron, rounded undersurface, and possibly also the elbow-shaped posterior lateral plate.

Order *COCCOSTEIFORMES*

Sub-Order BRACHYTHORACIDI

Family Buchanosteidae

Diagnosis. Broad-headed brachythoracids with long nuchal-paranuchal region and short wide central plates. Ventral surface of neurocranium, vessels, and cranial cavity invested with perichondrial bone, the post-ethmoid region probably ossified in a single piece, with wide suborbital shelves, shallow and broadest at base in cross-section between the two postorbital processes; posterior process single, pierced by large vein. Occipital region wide and extremely short.

Remarks. There seems little point in extending the diagnosis in view of our limited knowledge of this form and of the corresponding parts in other brachythoracids.

Genus ***BUCHANOSTEUS*** Stensiö, 1945

Diagnosis. As for family (only genus).

Remarks. The genus *Buchanosteus* was proposed by Stensiö (1945: 8, 24) for the arthrodire described by Hills (1936) as *Coccosteus osseus* on the grounds that the endocranial structures shown by the holotype resembled those of a dolichothoracid (arctolepid) and differed apparently very widely from such structures as were known among brachythoracids. However, specimen P.27071, which is surely congeneric with Hills's, displays a number of new features that in my opinion show that Hills was undoubtedly right in so far as he interpreted his fossil as a brachythoracid (see pp. 274–6 *infra*), and at the same time it adds very materially to our knowledge of the endocranial structures of the group.

The form of the skull-roof, the position of the eyes, and the pattern of the plates composing the roof and of the sensory canal system clearly stamp these fishes as brachythoracids—in particular we may note the relationships of the eyes to the preorbitals, the wide-based nuchal, the short occipital region, and the absence, as shown by the sensory canals, of lateral extrascapular elements in the paranuchals, the last a point on which Stensiö (1945: 42, 48, 55) has laid some emphasis.

GENOTYPE. *B. confertituberculatus.*

Since by common practice varietal names have the same standing as those of sub-species (cf. *Int. Rules Zool. Nomen.*, 1926, art. 12), Hills's specific epithet *osseus* should not be used. His holotype is also the holotype of Chapman's (1916: 213) *Phlyctaenaspis australis* var. *confertituberculata*, and as it is apparently impossible to say whether this specimen is conspecific with the types of McCoy's still earlier *Asterolepis ornata* var. *australis* (Hills, 1936: 214), Chapman's varietal name must stand for the species. The name of the genotype is therefore *Buchanosteus confertituberculatus* (Chapman).

Buchanosteus murrumbidgeensis sp. nov.

(PL. 30; PL. 31, FIGS. 1, 2; TEXT-FIGS. 20–27)

DIAGNOSIS. A *Buchanosteus* with long antero-lateral (postorbital) margin of skull-roof and short postero-lateral margins. 'Preopercular' sensory groove very short. Ornamentation of dermal bones consisting of numerous irregularly arranged tubercles capped with numerous fine radiating ridges and having a smooth waist passing below into coarse irregularly radiating ridges.

MATERIAL. The holotype (a diagonal slice of the skull, P.27071) and a fragment of the median dorsal plate of a smaller individual, P.27072.

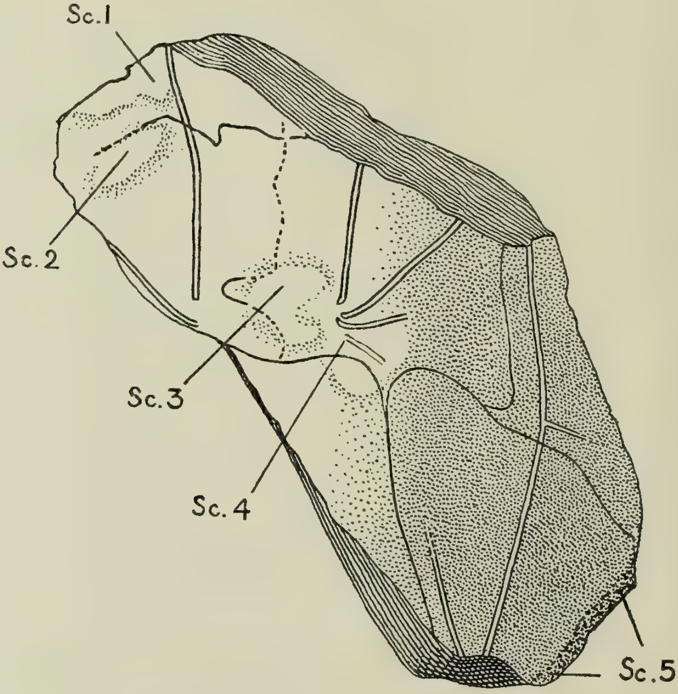
FORMATION AND LOCALITY. Middle Devonian: Parish of Taemas, Murrumbidgee River, N.S.W.

DESCRIPTION. The holotype belongs to a much larger individual than that of *B. confertituberculatus*, if Chapman's (1916: 213) original dimensions and not Hills's (1936: expl. pl. iii) magnification is correct; for Chapman gives the approximate width of his fossil as 69 mm., whereas the new fragment represents a skull about 125 mm. over the curve at the paranuchals. This specimen, being diagonally cut (Pl. 30, fig. 1; Text-fig. 20), shows part of all the component plates of the skull-roof except the rostral and the postmarginal, and a very fair reconstruction of the roof may be made (Text-fig. 21). The whole of the anterior and most of the posterior margins are missing, as are also the preorbital and postorbital processes. The individual bones are strongly fused together, but in the hinder part the sutures are clear enough; elsewhere they are less certain owing to the dense ornamentation, cracks, and the scars due to injuries received during the lifetime of the animal.

The specimen has been carefully developed in acetic acid in an effort to clear the internal structure, but the ossification is so very light that the process had to be stopped before completion to avoid serious damage to the specimen (Text-fig. 22).

The skull-roof has a perfectly straight median longitudinal profile so far as it is preserved, and transversely is flattened on top but strongly curved downwards at the sides (Text-figs. 23, 24). Except for the small postmarginal plate, which has not been detected, the right lateral margin is complete, including the lateral-posterior corner and as far forwards as the postorbital prominence. On the left side part of the upper margin of the orbit is preserved.

The whole surface is closely covered with small tubercles, most of which have been worn smooth or damaged during the lifetime of the fish. However, a substantial proportion are intact (Pl. 30, fig. 2) and show that the caps of the tubercles were domed or bulb-shaped and covered with numerous fine radiating ridges. Below the cap there is a slight, smooth waist which passes into the base formed of up to twenty coarse irregularly radiating and almost smooth ridges like the roots of ancient trees. These ridges coalesce with those of neighbouring tubercles to form a coarse network on the intertubercular spaces, in the meshes of which open conspicuous external pores from the middle layer.



Buchanosteus murrumbidgeensis sp. nov.

Text-fig. 20. Diagonal slice of skull-roof, original condition with fractures omitted, but showing scars (Sc. 1–5). The holotype, P.27071, nat. size.

The crude microstructure of the bone is readily seen in the fractured surfaces and corresponds well enough with the descriptions of Heintz (1929: 27, fig. 5, pls. xxii–xxiv for monaspids) and Gross (1930: 135, pl. ii, figs. 10, 12, 13; 1935: 25, for *Coccosteus*). Heintz divides the bone into four layers (basal, canal, reticular, and surface), Gross into three (basal, spongiosa, and tubercular), both emphasizing the gradual transition between one layer and the next. Everywhere in this specimen the surface layer is extremely thin in the intertubercular spaces where the external pores are conspicuous, but it forms the whole of the caps of the tubercles, appearing as a dark, dense substance without any visible perforations. The spongiosa forms practically the whole thickness of the bone, for a lamellated basal layer does not seem to be developed except for a single very thin sheet indistinguishable from the perichondrial bone of the endocranium with which it appears to be continuous. The spongiosa varies in texture and thickness from place to place. Sometimes, as in the flat middle part of the head near the pineal region where the bone is thin, a lower *canal zone* and an upper *reticular zone* may be distinguished, while farther back the thick bone of the nuchal plate shows a thin horizontal cavity which tends to split the upper part in two. Near the front of the central plate, at the start of the downward curve, the lowest part encloses some relatively large vessels, some of which are seen below as discrete tubes of perichondrial bone where they passed upwards through the unossified endocranium (*cf.* cutaneous vessels; Stensiö, 1945: text-fig. 1). On the sides of the head the bone again thins somewhat before passing into the thick marginal area where the whole of the spongiosa is uniformly trabecular, with gradual and relatively slight decrease in size of mesh from bottom to top. But below large vessels seem to be adhering to the roof. A remarkable feature shown by the skull-roof is that in places the thin outer tubercular surface layer has been formed as skin without any spongiosa over a similar layer with smaller tubercles, which may be readily exposed by simply chipping the outer layer away (Pl. 30, fig. 3). That this is an abnormal development seems probable, but so far as I am aware no account of the means of growth of arthrodire plates has been published.[1] For that matter, no remains of really juvenile arthrodires have been described, the smallest being about half-grown (cf. Watson, 1934: 442), but even these are very rare, so that a true growth-series is not available. Since the tubercles of the ornamentation appear to increase with size and the thickness of the surface layer does not, this layer was possibly normally resorbed and redeposited. The battered condition of this piece of skull suggests that the fish may have been very old, and the apparent physiological lapse suggested by this abnormal growth due to senility.

The outlines of the component bones are given in Text-fig. 20 and the whole restored in Text-fig. 21. The form of the bones at the back is perfectly clear, and most of the others may be accepted with some confidence. The very large nuchal is trapezoid and slightly concave in front, the equally large paranuchals broadly triangular and diagonal, the centrals very short and wide, but the sutures with the postorbital are the least satisfactory. The posterior and posterior orbital margins are restored from Hills's (1936: text-fig. 6) reconstruction of *B. confertituberculatus*.

The skull-roof is deeply incised by the grooves of the sensory canals, which closely resemble in their distribution those of coccosteids (e.g. Stensiö, 1925: figs. 24*a*, *b*), particularly of *C. decipiens* as figured by Heintz (1931*a*: 295, fig. 3). On each side the groove of the supraorbital canal (*soc*) runs forward from the posterior-mesial area of the central plate, diverging from its fellow as it passes on to the preorbital. A little farther back from the same spot (which is presumably the centre of ossification of the central plates, although this cannot be seen) the central sensory groove (*csg*) passes obliquely forwards and outwards towards the postorbital plate, where doubtless it joined the infraorbital groove (*ioc*). This groove is seen to run backwards over the margin to continue as the main lateral line groove (*lc*) to the postero-median border of the paranuchal plate, giving off in the process a short preopercular groove (*poc*) a little in front of the hinder border of the marginal plate.

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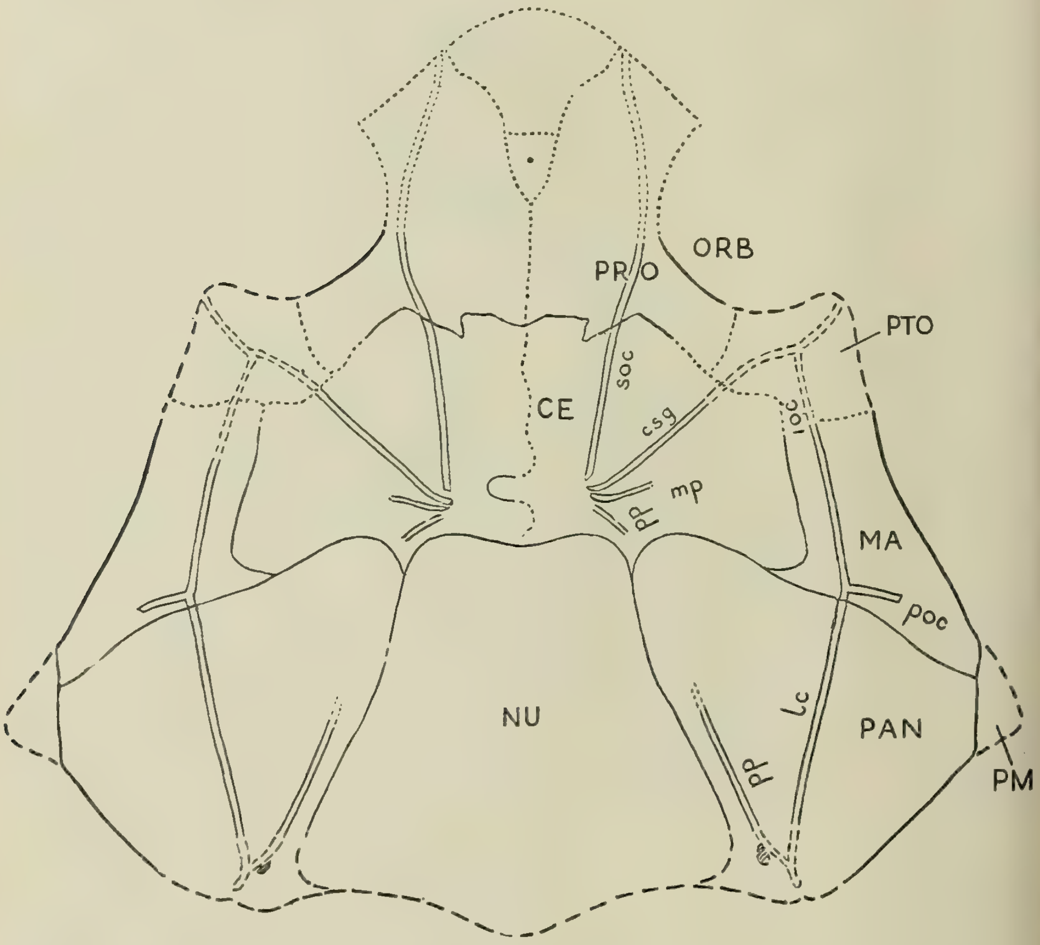
[1] However, Dr. T. Ørvig kindly informs me that he considers that this is the normal method of growth in the arthrodire exoskeleton.



Buchanosteus murrumbidgeensis sp. nov.

Text-fig. 21. Restoration of skull-roof flattened out, based on holotype, P.27071. Parts based on Hill's (1936) specimen of genotype shown by broken lines. Nat. size.

(For explanation of lettering see pp. 303–304.)

A third groove on the central plate is that of the short transverse median pit-line groove (*mp*), and there was yet a fourth, the groove of the anterior part of the posterior pit-line (*pp*), as in Stensiö's restorations of *Coccosteus* (1925: 174, fig. 24*a*) and *Kujdanowiaspis* (1945: 34, fig. 8). This part is almost obliterated by scarring, but the groove of the posterior part of this pit-line clearly runs forwards from the posterior end of the main line (with which it was undoubtedly joined) alongside the nuchal plate fading out at about the middle of its length.

Not the least interesting point about this specimen is the scarring of the roof-bones, due to wounds received either in fighting, or more likely in predatory attack. Immediately above the left orbit, where the preorbital, postorbital, and central plates should meet, there is evidence of damage of two kinds, gouging and shearing (Pl. 30, fig. 1). On the preorbital plate the spongiosa has been gouged out and then repaired most incompletely and irregularly, sometimes by regrowth of the spongiosa, apparently without the surface layer and to the extent of making a slight bump above the normal surface, while over most of the affected area the depression in the spongiosa has not been filled in, but instead scattered, fully formed tubercles of the surface layer cover the rough surface of the depression (Text-fig. 20; Sc. 1). The hinder part of this area has been sheared off at a later date since the damage appears to affect the previous repairs, while a similar slicing wound on the neighbouring area of the central plate ends in a clear straight cut (Sc. 2).

In the centre of the skull-roof (Pl. 31, fig. 2), on the hinder part of the suture between the central plates, is evidence of larger wounds. The earlier is again a gouged pit which has been imperfectly repaired (Sc. 3), partly by a thin covering of the external glassy layer with scattered tubercles and partly by secondary deposition of spongiosa, which further formed an irregularly raised rim around the hole, but on the right side, where the four grooves converge, the primary ornament has again been planed off and with it the secondary rim of the original wound (Sc. 4). The paranuchal border is also planed off (Sc. 5).

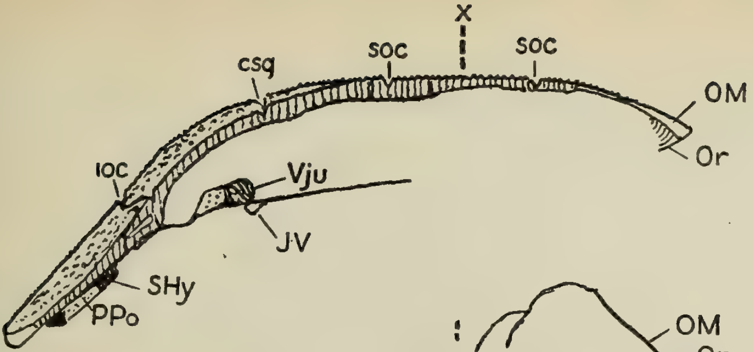
The earlier set were gouged out by powerful pointed teeth belonging to a creature that was certainly a good deal larger than its victim. It is not the sort of wound that one would expect from an arthropod (or any other invertebrate, however large) and may be considered certainly due to the bite of a vertebrate predator, i.e. another fish. Contemporary sharks, palaeoniscoids and acanthodians are not known from these beds as yet and in any case would, unless they were excessively big, have inflicted a different type of injury giving a more linear scar; *Dipnorhynchus* (Hills, 1941) presumably had the usual dipnoan crushing dentition and could hardly have this effect; but the anterior prehensile tooth-plates of a large coccostean with a dentition like that of *Dinichthys* is just the right instrument and the two holes suggest that our creature was held diagonally across the head by the widely separated gnathals (see Heintz, 1932: 191, fig. 81; Watson, 1934: text-figs. 3, 4). How it managed to get away is another story, but that it did is evident enough from the repairs.

The second set of markings was obviously considerably later in age, since the first set had by then completely healed, and as they show no signs of repair they may have been made at the time of death, although in themselves not serious enough to have been fatal, or they may have been made *post mortem*, and Sc. 4 may even be an artifact. If contemporary, it is not quite so clear what kind of teeth rasped these patches, but the cut which bounds the orbital wound (Sc. 2) suggests that they were the result of lateral movement by a blade, possibly by the victim struggling to free itself when caught by the posterior superognathals of yet another arthrodire. The only large contemporary arthrodire of which we have evidence is *Taemasosteus*, but although a good deal bigger than this fish, the specimen of which we have evidence was hardly big enough to have caused the first set of wounds, at any rate.

If some of these markings are indeed the result of attacks by other arthrodires, it certainly supports the idea that some arthrodires at least were active predators and not just carrion-feeders and conchophages (see Geuenich, 1939: 27; Stensiö & Jarvik, 1939: 266).

The undersurface of the fragment is most interesting since the base of the neurocranium was invested with a perichondrial bone-layer, which also lined the cavum cerebrale cranii and the canals of the vessels and nerves, as noted above. Unfortunately the part preserved is no more than the right posterior corner of the postethmoidal bone (Pl. 31, fig. 1; Text-figs. 22–24), from just behind the anterior postorbital process to the supravagal process; but with the holotype of *B. confertituberculatus* described by Hills (1936) one can obtain a fair general idea of the outline of the whole (Text-fig. 27).

The perichondrial bone lining the smaller canals is extremely thin, but that covering the undersurface of the postethmoidal bone is much thicker and shows a middle cellular layer. Laterally, above where the perichondrial bone meets the skull-roof, the spongiosa of the latter is thickened and contains one or more short longitudinal cavities (Text-fig. 23). The dermal skull-roof forms the roof of the shallow neurocranium, the thin basal layer being indistinguishable from the perichondrial bone with which it is continuous laterally. Owing to the investing bone the details of the side of the neurocranium between the two postorbital processes cannot be seen, but the front view, just behind the anterior process, shows it to be broader below than above, in distinct contrast to that of the arctolepid *Kujdanowiaspis* (Stensiö, 1945: text-figs. 4, 5). The undersurface is flat longitudinally (Text-fig. 24), the roof slopes on an even curve to the supravagal process, and there is no sign of a supranuchal depression. The neurocranium was deeply embayed between the two postorbital processes, but externally the covering bone runs evenly to the skull-roof, forming a rounded depression on which a number of clearly marked ridges run laterally outwards, possibly connected with the ligamentous attachment of the hyomandibula (*cf.* Stensiö, 1945: 22). The posterior postorbital process was single and carried the large vein (SHy)which certainly emptied into the jugular (VJu). Stensiö (1925: text-fig. 6) identified this vein in *Macropetalichthys* as the hyoid vein, but Holmgren (1942: 170) in his great work on the heads of fishes criticized this identification on the grounds that in sharks the hyoid vein enters the jugular farther behind the postorbital process and moreover the jugular itself is never enclosed in a canal in the cranial wall proper. He suggested that this vein and Stensiö's jugular form the v. subpostorbitalis. More recently in *Kujdanowiaspis* Stensiö (1945: 32, text-fig. 6, &c.) named this vein the 'v. posthyoidea lateralis', coming from the posterior dorsal parts of the cheek, and placed the hyoid vein still farther forwards in an even more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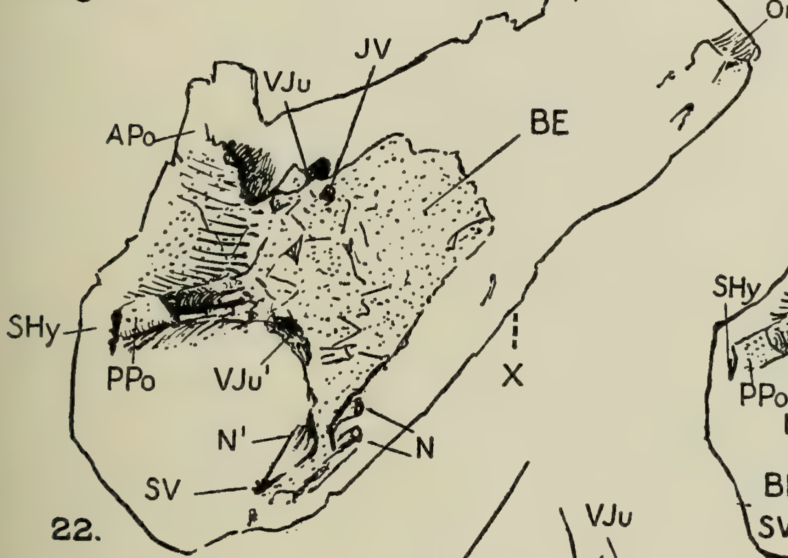
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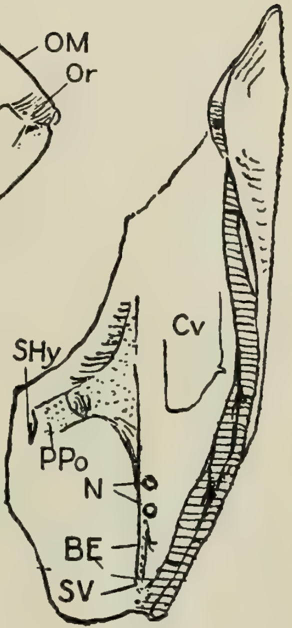
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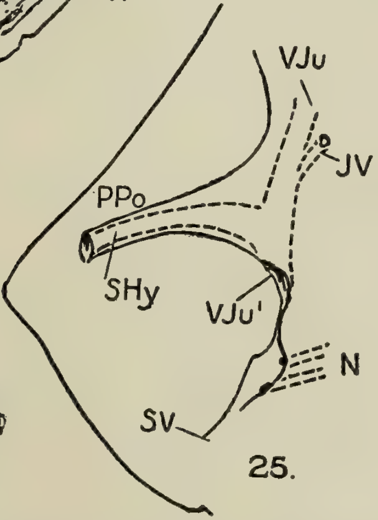
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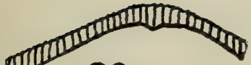

26.

Buchanosteus murrumbidgeensis sp. nov.

Text-fig. 22. Ventral view of holotype, showing part of undersurface of neurocranium. P.27071, nat. size.

Text-fig. 23. Direct front view of same.

Text-fig. 24. Direct left lateral view of same.

Text-fig. 25. Restoration of right posterior corner of undersurface of same, showing passage of vessels in neurocranium.

Text-fig. 26. Cross-section of small median dorsal plate. P.27072, nat. size.

(For explanation of lettering see pp. 303–304.)

unsharklike position, immediately behind the exit of the jugular vein from the anterior postorbital process. Holmgren's objection would clearly be valid if arthrodires were simply selachians, which they are not, whatever their relationships may be (Holmgren, 1942: 161; Stensiö, 1950: 38; Watson, 1950: 42); while the vessel in this form seems too big for his interpretation. In spite of its rather posterior position it may well be that this is the hyoid vein as Stensiö first thought, for his 'posthyoidea lateralis' has no modern counterpart comparable in size that I know.[1] The covered-in jugular is seen in the front view lying immediately on the perichondrial bone of the undersurface and just behind it receives a smaller vein running upwards and backwards from the undersurface. The jugular vein passed out behind in the middle of the embayment between the posterior postorbital and the supravagal processes and formed a short groove or notch on the undersurface along the margin (VJu′), immediately behind which is another groove (N′) containing the external openings of the vagus canals which are themselves visible on the inner broken surface (N). The lateral wall of the embayment is not seen except for a short distance below and behind the vagus openings, where it is almost vertical, and may not have been ossified, since the bone of the undersurface appears to end in a clear margin, corresponding to the supravagal ridge in *Kujdanowiaspis*.

Other features on the undersurface, which is much cracked, are vermiculating grooves of small blood-vessels.

The form of the hinder margin can be deduced from the shape of the skull-roof, since the internal articular surfaces must have been on the line of the external cervical joints. The occipital region was therefore extremely short.

The form of the orbitotemporal region may be confidently restored from what is known of the holotype of *B. confertituberculatus* (Hills's '*Coccosteus osseus*'), and here we may note the wide suborbital shelf (SS) and the small median cusp (MC) of the concave anterior margin, presumably developed in connexion with the internasal septum.

The fragment of a median dorsal plate (Pl. 30, fig. 4; Text-fig. 26) seems to belong to this species by reason of the similarity of the ornament, but to a much smaller individual showing an unexpectedly ridged back.

REMARKS. The most marked features of the genus *Buchanosteus*, as we know it, are the large nuchal and paranuchal plates, the short centrals and the, partly at least, ossified ventral surface of the endocranium; while this species is apparently distinguished from the genotype by the longer postorbital margin, the shorter paranuchal margin, and the very brief preopercular groove. The skull-roof is that of a typical brachythoracid, and there can be no doubt that the creature belonged to that group. Hitherto, besides a brief account of the nasal region of *Coccosteus canadensis* (Stensiö, 1942: 21) the only endocranial ossifications described in this group have been the fragmentary ethmoid and otic regions in *Pholidosteus* and the occipital in *Leiosteus* (Stensiö, 1934*a*), both aberrant Wildungen genera (Gross, 1932). Stensiö (1945: 24), on the basis of Hills's (1936) description, erected the genus *Buchanosteus* for '*Coccosteus osseus*' and referred it to the dolichothoracids (arctolepids) on the grounds of the similarity of the postethmoidal bones as then described. The new material shows, however, that although there are similarities, these are no more than one would expect in two groups of arthrodires, and there are important differences, among which we may note the larger suborbital shelves, the single posterior postorbital process, the complete enclosure of the jugular vein in the two postorbital processes, the very short occipital region, the entirely different cross-section in the postorbital region and, by no means without significance, the median ethmoid cusp.

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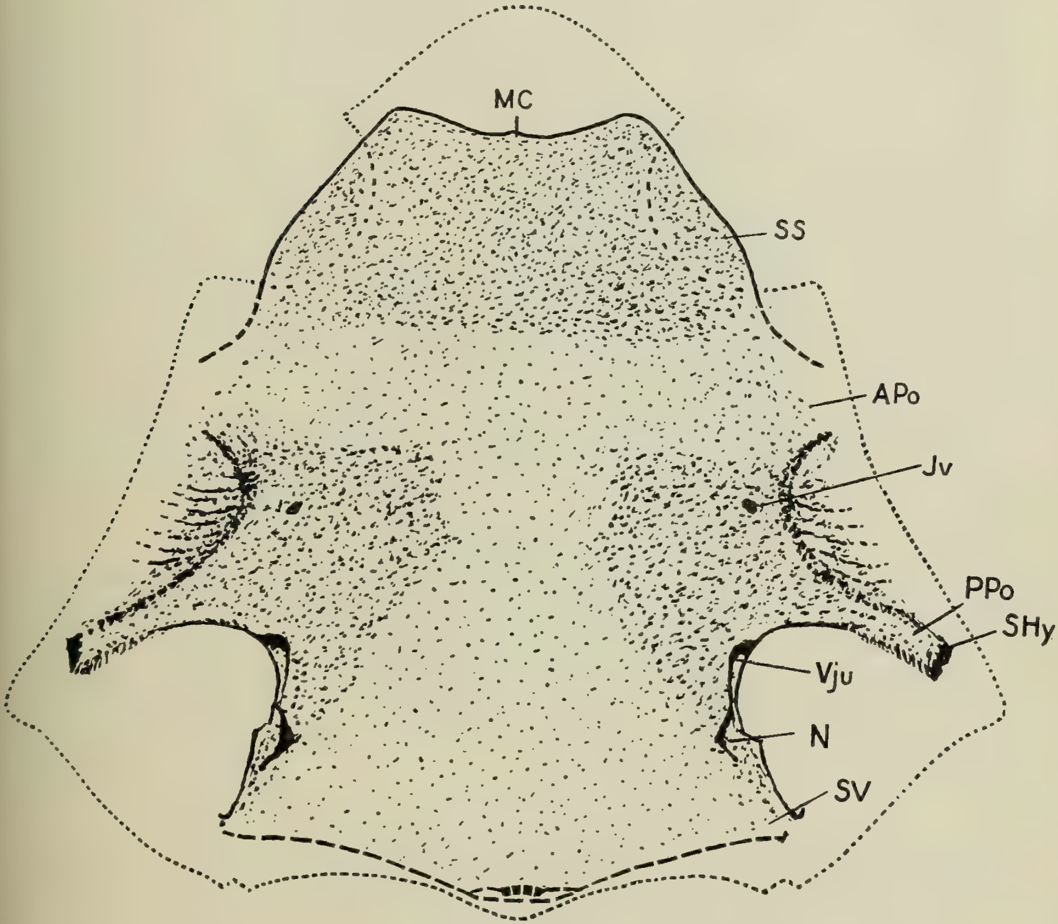
[1] Professor Stensiö kindly informs me that he now finds that there is no canal piercing this process in *Kujdanowiaspis*, which further emphasizes the difference between the two types of skull.



Buchanosteus murrumbidgeensis sp. nov.

TEXT-FIG. 27. Restoration of undersurface of neurocranium flattened out with outline of skull-roof superimposed; orbito-temporal region based on Hills's (1936) specimen. Known areas heavily stippled.

(For explanation of lettering see pp. 303–304.)

It is not altogether easy to reconcile this neurocranium with what has been published of the neurocranium in *Pholidosteus*, the only brachythoracid of which we have an account of comparable parts. The fragmentary otic region of *Pholidosteus* (Stensiö, 1934*a*; pl. 4, figs. 2–4; text-fig. 7), in spite of its breadth, appears to represent only the anterior postorbital process (of which nothing is known in *Buchanosteus* except the proximal part of its hinder margin), and this requires that the identification of some of the canals be reconsidered. For instance, that labelled *c.hy* is possibly that of the 'vena mandibularis' in *Macropetalichthys*, and not the v. hyoidea, which would have traversed the presumably cartilaginous posterior process, entering at *cx*, while the main jugular canal, instead of leaving the anterior process at *ju*, is entirely enclosed and passes out at *cy*. The ethmoidal region of *Pholidosteus* (Stensiö, 1934*a*: pl. 11, fig. 5; pl. 12, figs. 1, 2; text-figs. 1–3), is so laterally compressed and modified by the enormous, forwardly-placed orbits that comparison with the imperfectly known dorso-ventrally flattened region of *Buchanosteus* cannot be usefully made. One may doubt whether the differences are other than those due to specialization in different directions, although Stensiö (1942: 21) specifically states that this region in *Coccosteus canadensis* is fundamentally as in *Pholidosteus*.

As for the occipital region, all we know is that in *Buchanosteus* it was extremely wide, even shorter than in *Leiosteus* (Stensiö, 1934*a*: 37), and much shorter than in the arctolepid *Kujdanowiaspis*.

Family TAEMASOSTEIDAE

DIAGNOSIS. Brachythoracid arthrodires having the paranuchal plate long and leaf-shaped, with all its sides evenly convex and all but the inner posterior angle rounded, overlapped only by the nuchal plate which it exceeds in length.

Central plates narrow behind, marginal plates very long and postmarginal plates large. Ornamentation finely pustulate. Main lateral line groove deeply incised and diagonal in direction, connected at posterior end with extremely short posterior pit-line groove.

Genus ***TAEMASOSTEUS*** nov.

DIAGNOSIS. As for family (only genus).

GENOTYPE. *T. novaustrocambricus* sp. nov. (only species).

Taemasosteus novaustrocambricus sp. nov.

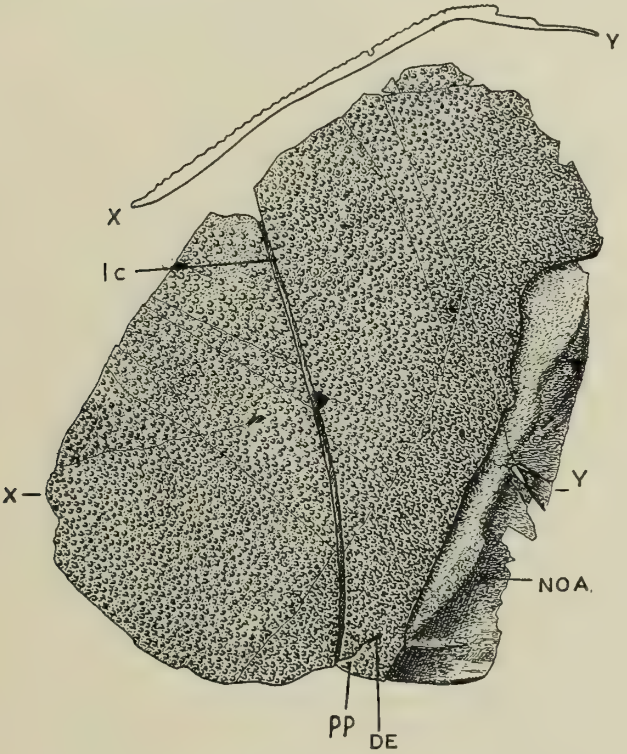
(PL. 31, FIG. 3; TEXT-FIGS. 28–30)

DIAGNOSIS. As for family and genus (only species).

MATERIAL. Unique holotype, a left paranuchal plate (P.27070).

FORMATION AND LOCALITY. Middle Devonian: Parish of Taemas, Murrumbidgee River, N.S.W.

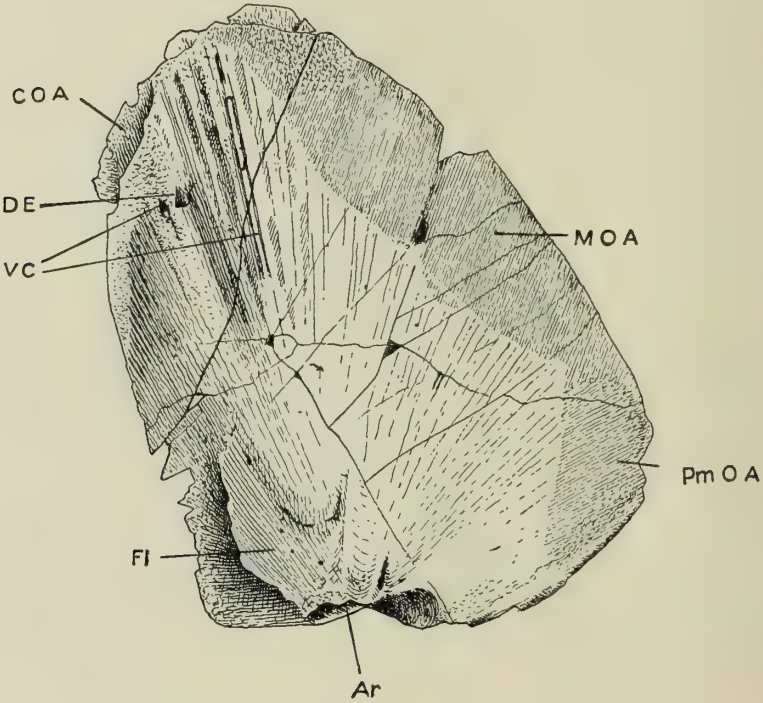
DESCRIPTION. The specimen was originally attached by the external surface to its matrix, a large piece of hard, grey, marine limestone containing the remains of numerous brachiopods. The matrix was, however, removed with acetic acid and the whole bone is now beautifully exposed on both surfaces (Text-figs. 28, 29). It is in very fine condition, apparently quite uncrushed, and apart from slight marginal chipping owing to the extreme thinness of the bone there, and the loss of part of the articular process and hinder margin, it is complete. The plate is 9·2 cm. long and a little more than 6·5 cm. in width, so that the fish was a large one. For a paranuchal the plate is distinguished by the simplicity of its outline, for all the margins are virtually entire, showing a continuous but varying convex curvature, except at the posterior inner corner which is angular, and the notch where the lateral line runs on to the marginal. The plate is gently bowed lengthwise, but is much more strongly convex across the breadth, being roughly divided by a rounded angle of about 25° running directly forwards from the start of the sensory canal into a long, narrow, median surface that formed with the nuchal a horizontal flat crown to the head and a large sloping lateral area.



Taemasosteus novaustrocambricus gen. et sp. nov.

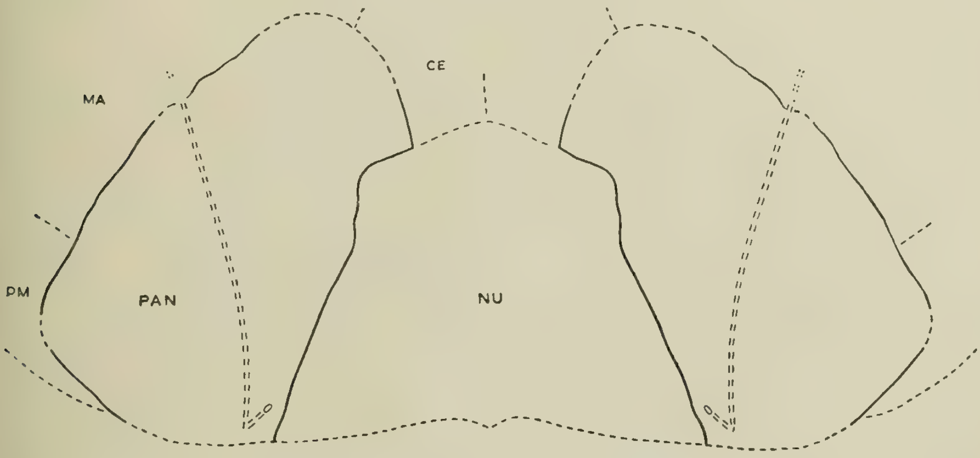
TEXT-FIG. 28. Paranuchal plate, with cross-section at *X–Y*. The holotype, nat. size. (For explanation of lettering see pp. 303–304.)

The whole of the exposed surface is covered with fine tubercles which consist individually of a small shining conical cap decorated with numerous fine radiating ridges on a very much wider (sometimes three or four times as wide) roughened base passing into numerous irregular roots which cross and anastomose with those of its neighbours, and in between which are the external openings of tubuli (Pl. 31, fig. 3). However, the surface is seldom fresh and usually the fine ridges are worn away and the caps smooth. The upper surface of the overlapped area shows the openings and part of the vermiculating tubules of the spongiosa, very much as if it were a cut surface. The exposed surface is crossed by the deeply incised main lateral line groove which runs forward from the articulation near the nuchal overlap and quickly curves outwards to run diagonally to the outer margin at about two-thirds of the way along its length. At its hinder end it gives off a very short, curved, and much shallower branch, the posterior pit-line groove, ending in a longish pit. This pit was the dorsal aperture of the ductus endolymphaticus which ran forwards through the bone underneath the margin of the nuchal overlap, forming a short, increasingly conspicuous ridge on the anterior part of the undersurface. The lower, anterior aperture is not preserved, but it cannot have been far from where the canal now ends (DE, Text-fig. 29).



Taemasosteus novaustrocambricus gen. et sp. nov.
TEXT-FIG. 29. Undersurface of holotype.
(For explanation of lettering see pp. 303–304.)

The area overlapped by the nuchal plate is remarkable for it shows that the nuchal was very much shorter than the paranuchal. This area is flat in front but curves down mesially behind where it is divided into two by a longitudinal step, which deepens and then curves into the ornamented lateral margin near the hinder border of the plate. Here also the lower part of the area rises owing to a thickening of the bones for the formation of the articular socket. This part of the plate is much the thickest and the undersurface shows that here was the centre of ossification, as indicated by the radial structure of the bone. The radial structure is indeed remarkably clearly shown, with one or two of the vascular canals of unusual size, particularly one running close to the foramen of the ductus endolymphaticus on its mesial side and another on the other side of it rather farther away (VC, Text-fig. 29).



Taemasosteus novaustrocambricus gen. et sp. nov.
TEXT-FIG. 30. Restoration of posterior half of skull, flattened out. × ⅔ approx.
(For explanation of lettering see pp. 303–304.)

However, the most conspicuous feature on the lower side of the plate, which of course is concave, is a thin, deep lamina of bone (Fl) that forms part of the support of the articular socket, which is itself missing. The lamina lies at a low angle, about 10°, directed towards the nuchal margin with which its base is roughly parallel, although its extent towards the centre of the head is uncertain. That the articular parts were massive is indicated by the wide, rounded ridge which runs from the hinge outwards along the posterior margin, flattening as it goes.

Along the thin, outer margin there are wide areas devoid of the basal layer showing the degree of overlap on to the marginal plate (MOA) and the postmarginal plate (PmOA). The former is extremely long, equal to nearly three-quarters the length of the plate and 2½ times the postmarginal overlap, which it meets at nearly a right angle. On the other hand, the area of overlap on to the central plate in front is short and if the nuchal plate is properly orientated, the central plates must have been unusually narrow (Text-fig. 30).

The microstructure of the bone is interesting. The spongiosa forms almost the whole of the bone, for the basal laminated layer is exceedingly thin and usually rubbed away, while the surface layer seems confined to the caps of the tubercles.

The spongiosa varies in texture from place to place. Near the articulation, the broken surfaces show the bones to be almost solid with fine tubules, and at the articulation itself it is vertically laminated. Away from this point the thick margins at each end of the overlapped area are very spongy, but the thin margin in between shows distinct division into two or three laminae. As in many arthrodires a marked feature of the bone is the radial arrangement and straightness of many of the canaliculi in the lowest part of the spongiosa. The presence of these canals (Heintz's 'ossification rays', 1932: 122, 172, &c.) on the undersurface of the bone has already been noted and they are particularly clear where the basal layer on the surface is slightly damaged; but even where this is present the canals pierce this surface to form open pores of various sizes, and are particularly numerous near the hinge or centre of ossification. The great majority of these vascular canals are very fine, as fine as the vermiculating canals with which they are associated, but they seem to grade up into much larger canals (VC) of which the largest, measuring nearly 2 mm. in diameter, has been identified with the ductus endolymphaticus.

Remarks. Although the exact orientation of this paranuchal plate cannot be determined with complete accuracy owing to the absence of the hinge area, we may make a reasonable attempt at restoring part of the back of the skull (Text-fig. 30), which seems to have had several unusual features. The large size of the paranuchals relative to the nuchal plate is, so far as I know, unique, as is also its rounded shape.

The marginal plate must have been unusually large, and recalls in this respect certain of the Wildungen genera, such as *Rhinosteus* and *Leptosteus* (Gross, 1932: text-figs. 7, 12), and further resembles them in the extent and position of the postmarginal plate. The presumed narrowness of the posterior end of the central plates is also seen in *Leptosteus* which is a much laterally compressed form, whereas *Taemasosteus* certainly is not; but these resemblances are interesting probably only as showing that this form comes within the known limits of generic variation in the brachythoracid arthrodires, and not as indicating closer affinity to any particular form or forms.

Brachythoracidi *incertae sedis*

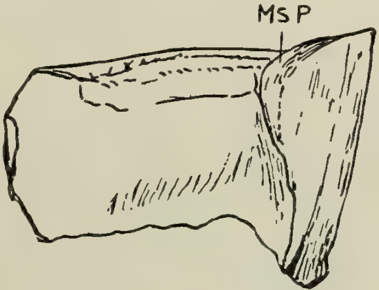
(Text-figs. 31–35)

Material. An isolated left posterior superognathal (P.27074).

Formation and locality. Middle Devonian: Barber's, Goodradigbee River, N.S.W.

Description. As received, only a small part of this specimen was exposed, but it has now been completely disengaged from its matrix by means of acetic acid. The length is only 9·2 mm. Seen from above (Text-fig. 33) the bone has in front a strong mesial process. The hinder margin of this process is at right angles to the body and the anterior runs forwards and inwards at about 45°. Most of the anterior outer face is missing, but behind the break the outer margin continues backwards in a gently sinuous curve to meet the inner side in a point.

The anterior face of the mesial process is that in contact with the anterior superognathal (cf. Heintz, 1932: 148, text-figs. 28, 29). It is roughly triangular, narrowing and sloping gently inwards and downwards to the origin of the blade. The broad upper part is more or less flat, but a groove develops below along the front edge, which is straight but somewhat sloping.



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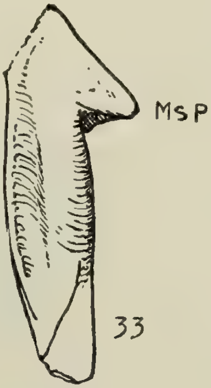

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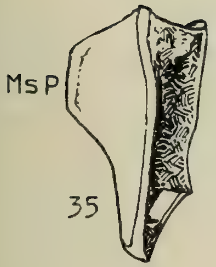

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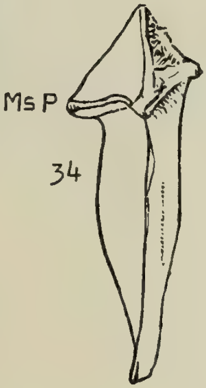

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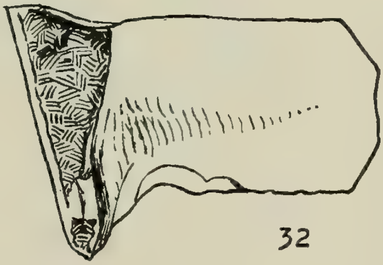

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Text-fig. 31. Left posterior superognathal of undetermined brachythoracid, inner view. P.27074, ×5.

Text-fig. 32. The same, outer view.

Text-fig. 33. Palatal (dorsal) surface.

Text-fig. 34. Direct oral (ventral) view.

Text-fig. 35. Front view.

(For explanation of lettering see pp. 303–304.)

The corresponding face on the outer side has decayed (Text-figs. 32, 35) except for a narrow vertical selvage along the front margin and a fragment below. The form of this face is uncertain, but the anterior selvage is transverse to the length of the bone and suggests that the upper part was rounded, although the fragment below shows a vertical division into two facets. The whole face is separated behind from the body of the plate by a low, nearly vertical ridge which runs to meet the median and mesial ridges in a point at the start of the blade.

The blade is single and in side view (Text-figs. 31, 32) is irregularly concave, running upwards and backwards in a wavy line and then curving round 45° to continue backwards to the hinder end. From below (Text-fig. 34) the blade is almost straight with a gentle inward curve towards the rear. The only shearing surface is in the form of two crescentic areas at the angle and on the outside (Text-fig. 32).

The posterior end is almost as thin as the blade and was apparently rounded without denticles.

The upper surface, by which it was attached to the palatoquadrate, shows a distinct longitudinal groove near the outer margin, which is raised and sharp, and there is a slight eminence over the mesial process but nothing so pronounced as that in *Dinichthys* (Heintz, 1932: text-fig. 28).

The break in the outer face shows, rather surprisingly, that this part of the tooth was hollow, or at any rate of very loose structure, with a distinct inner longitudinal wall under the groove on the attached surface.

REMARKS. This small, probably juvenile, plate shows sufficient resemblance to the corresponding plates of *Dinichthys* (Heintz, 1932: text-figs. 28, 29) to make its identification as a posterior superognathal clear, but it is very different in such detail as the form of the mesial process, the irregularity of the blade, and the external shearing-surface, &c. The plate is of about the same size as Watson's (1934: 440, text-fig. 1*c*) gnathal of 'a nearly full grown but not old specimen' of *Coccosteus decipiens*, but differs from all the figured plates of that and other species of *Coccosteus* (Gross, 1933*c*: pl. 2, figs. 12, 19; text-fig. 10; Heintz, 1938*a*: text-fig. 3) in the stronger but lower mesial process, in the absence of posterior and external denticles, and in the irregular form of the single blade. Indeed, it differs considerably from all the known posterior superognathals (cf. Heintz, 1931*c*: 247, text-fig. 4; Dunkle & Bungart, 1946: text-fig. 3; Dunkle, 1947: text-fig. 2A).

Finally, it is interesting to note that in *Pholidosteus* (Stensiö, 1934*a*: 25, 36, pl. 11, fig. 5, pl. 12, figs. 1, 2, text-figs. 3, 12) the impressions on the mesial face of the palatoquadrate together (*p*+*gr. psg*) correspond very well with the form of the attached surface of the new plate, *p* being the impression of the mesial process; but if this is correct, then obviously the palatoquadrate will not be as vertical in position as it was described.

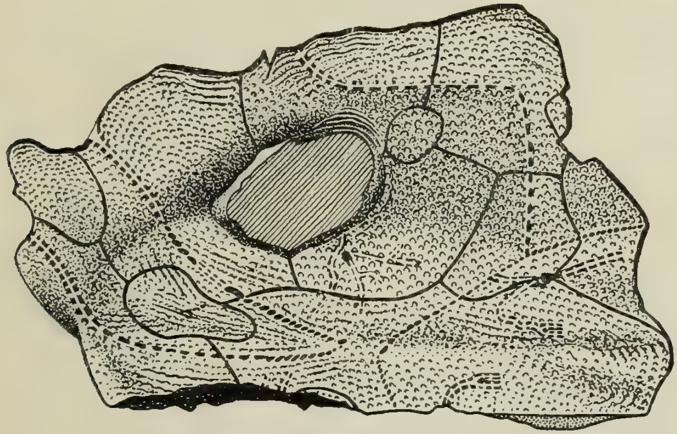
This plate is almost certainly that of a brachythoracid, although the only other arthrodire material found at Barber's was the arctolepid *Williamsaspis*. It is clearly too small, even though juvenile, to have belonged to *Taemasosteus*, but could have been carried by *Buchanosteus*. That, however, is just conjectural and it may represent yet another arthrodire genus.

III. THE GENUS *NOTOPETALICHTHYS* A. S. WOODWARD, 1941

Notopetalichthys hillsi A. S. Woodward

(TEXT-FIGS. 36, 37)

Recently I have had the opportunity of re-examining the unique specimen described by Woodward (1941) and am now able to add some details to the original description. The median length over the curve is exactly 10 cm. as preserved, but it is clear that the hinder margin of the centronuchal plate is not complete, as Woodward states, and doubtless continued farther backwards as in other petalichthyids (Stensiö, 1948: text-fig. 72). On the other hand, the whole rostral plate is now uncovered and projects forwards considerably (Text-fig. 36). The skull is distorted, being pushed diagonally towards the left anterior corner, but nevertheless, the original shape can easily be made out. The orbits and with them the whole central part of the head are raised rather abruptly, so that the marginal area forms a flattened brim, especially in front, but the skull is otherwise flat longitudinally.

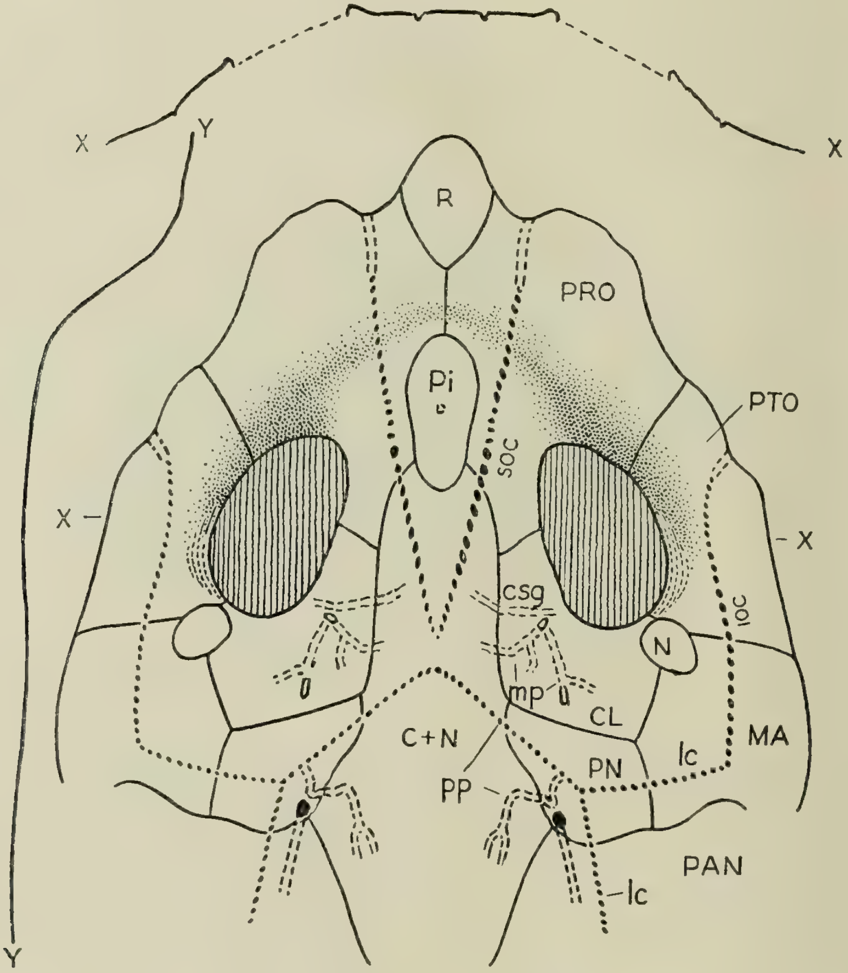


Notopetalichthys hillsi A. S. Woodward.

TEXT-FIG. 36. The holotype showing outlines of plates and sensory grooves. Nat. size.

The main sensory canal system is normal for the group, being like that in *Epipetalichthys*, without connexion between the supraorbital pair and the transverse posterior pit-line. It consists of series of well-defined pits, or grooves, merging into continuous canals marginally. In addition, on the lateral central, behind the eye and spilling on to the centronuchal plate are two sets of shallow pit-line grooves: a slightly curved transverse groove that may be the remnant of the central sensory groove eliminated by the inward migration of the eye, and an irregularly ramifying series immediately behind representing the median pit-line. Still farther behind, coming off inwards and backwards from the posterior pit-line canal is another short irregular groove passing very close to the opening of the ductus endolymphaticus and bifurcating distally; while from the opening itself, which is just inside the margin of the anterior paranuchal plate, a short groove runs straight backwards and slightly outwards on the posterior paranuchal.

The outlines of the component bones are now clearly to be distinguished and form a very characteristic pattern. The jutting rostral is separated for a considerable distance by the preorbital plates from the rather elongated pineal plate, which bears a central macula. The bent, diagonally disposed, lateral central plate (CL, Text-fig. 37), with ramifying sensory grooves, occupies nearly half of the margin of each very large orbit. Just behind the orbit, at the junction of the lateral central, postorbital, and margin plates, is a small ovoid plate, but whether this is a diagnostic character of the species present on both sides or an odd individual malformation cannot be determined, since the left side is not preserved.



Notopetalichthys hillsi A. S. Woodward.

TEXT-FIG. 37. Restoration of skull-roof. *X–X*, transverse and *Y–Y* median longitudinal profiles. (For explanation of lettering see pp. 303–304.)

An attempted restoration of the specimen is given in Text-fig. 37.

The genus is a well-marked one and may be briefly diagnosed as follows: a petalichthyid with marginal area of head depressed, especially in front of eyes, forming well-marked brim: orbits very large, somewhat oblique, placed on sides of slope from main raised area. Rostral plate small, projecting forwards and completely separated by the preorbital plates from the rather elongated pineal plate which indents the centronuchal. Lateral central plates oblique and somewhat L-shaped, forming large part of orbital margin. Small oval plate at junction of lateral central, postorbital, and marginal plates. Sensory canal systems in form of lines of deep pits in shallow grooves: supraoccipital canals not meeting posterior pit-line canal. Central sensory groove and median pit-line groove represented by short, shallow grooves, mainly on lateral central plates, the former simple and curved, the latter branched: similar grooves running irregularly from main posterior pit-line canal backwards and inwards past external opening of the endolymphatic duct.

GENOTYPE. The unique species, *N. hillsi* A. S. Woodward.

FORMATION AND LOCALITY. Middle Devonian: Goodra Vale, N.S.W

IV. PECTORAL FINS OF ARTHRODIRES

Direct evidence of pectoral fins is given by a number of arthrodires and their relations. Parts of the fin itself have been figured in an undetermined genus and in *Dinichthys* (Heintz, 1932: 197–8, text-figs. 85, 86, 90), *Coccosteus* (Heintz, 1938*a*: 20, text-fig. 5), *Rhachiosteus* (Gross, 1938*a*: 199, pl. ii, fig. 2; text-figs. 1, 5*a*), which are all Brachythoraci, in *Gemündina* and *Stensiöella* (Broili, 1933*a*: pls. ii, iii, text-figs. 3, 8), and *Pseudopetalichthys* (Broili, 1933*b*: 426, plate, fig. 1; text-figs. 3, 5; Stensiö, 1944: text-fig. 18); while the articular surface of the scapulo-coracoid is known in the brachythoracid *Enseosteus*, the arctolepid *Kujdanowiaspis*, the related *Palaeacanthaspis* (Stensiö, 1944), and in *Williamsaspis*. The pectoral fins were apparently long-based in all the brachythoracid examples, in *Coccosteus*, *Rhachiosteus*, Heintz's unknown genus, and *Enseosteus*; but were short-based in the arctolepids, in both *Kujdanowiaspis*, with its full body-armour, and in *Palaeacanthaspis* in which the body-armour is reduced. This clearly shows that the length of the fin-base is not to be correlated with that of the body-armour, and suggests that in arthrodires it had become a systematic rather than a functional character. The pectoral fins of *Williamsaspis*, although small proximally, are in fact long-based to the extent of being borne by a horizontal linear series of about nine separate basals on an elongated, slightly raised, articular ridge, reminiscent of the restored scapulocoracoid of *Enseosteus* (Stensiö, 1944: text-fig. 14) but on a smaller scale. Thus *Williamsaspis* still has obvious traces of a type of fin, long-based, lost in the more specialized arctolepids, but largely preserved by the brachythoracids. Stensiö (1944: 16) considers that the long-based type of the brachythoracids is the more primitive, which seems reasonable enough, but if the brachythoracids are primitive in their pectoral fins, they are certainly specialized in their body-armour to the extent that it is shortened laterally (Heintz, 1931*b*: text-fig. 10). The brachythoracids retained long-based pectorals but reduced their armour, while the arctolepids generally increased their armour to the extent of producing enormous pectoral spines, and reduced the pectoral fin-bases, so that the common ancestor of both groups must therefore have had full body-armour like the arctolepids but with a long-based pectoral fin like that of the brachythoracids in place of the spine. Heintz (1938*a*: 23, text-figs. 6, 7) has made an interesting morphological series of arthrodire reconstructions in which the long-spined forms precede the short-spined brachythoracids. In this series Heintz (1938*a*: text-fig. 6) gives '*Jaekelaspis*' a narrow fringe in the pectoral bay—'a slightly developed skin-fold'—which demands a slit behind in the spine and a space between the anterior lateral and anterior ventrolateral plates. Since such remnants could have had little functional value, Heintz was presumably anxious to retain in these forms some element of the fin in order to avoid the apparent 're-creation' in the adult of pectoral fins in the brachythoracids after the complete suppression of the lateral fin-folds in the arctolepids. But such a device could hardly have served such a purpose. A fin so specialized in respect of the spine and degenerate in respect of the web as that shown in Heintz's restoration of '*Jaekelaspis*' is certainly not going to develop later into a serviceable pectoral fin such as the brachythoracid arthrodires must have had, even if it was relatively stiff and acted largely as a gliding plane, capable only of slight movement as a whole or by undulation. It is true that we do not know the form of the very early stages of arthrodires which, like most juvenile ostracoderms, seem to have been unarmoured. Even if juveniles had retained pectoral fins eliminated in the adult, there is no evidence to show that the adult could have regained a character so lost, although Watson (1934: 448) has suggested the agency of a latent limb-bud for regaining a pectoral fin completely lost in ancestral forms. But what is more to the point, the arctolepids with long pectoral spines, such as '*Jaekelaspis*', are clearly the overspecialized end-terms of a series that could not have given rise to the progressive brachythoracids or to anything else, and their fate was the fate of all such series, extinction. Westoll (1945*a*: 350; 1945*b*: 383, text-fig. 3) has much elaborated Heintz's ideas on the development of arthrodire pectoral fins, grafting on to them his 'bone-jacketing' theory and providing the animals with a heterocercal tail. He supposed that the spines were extensions of the body-wall completely covered with dermal bone without even the fringe of fin postulated by Heintz, and that subsequently part of this pectoral body-extension was freed to form fin-membranes, while the prespinal lamella was considered to be possibly 'an integral part of the necessary structural bracing of such hydrofoils, the necessity for which disappeared with the differentiation of a controllable fin-membrane'. However, this 'fin-fold: jacketing: fin-release' sequence seems clearly to be disproved, at least in relation to the development of the arthrodire pectoral fin, by Stensiö's (1944) demonstration that the 'prespinal lamella' was the perichondrial ossification of the mesial surface of the scapulo-coracoid cartilage, and that the pectoral fin-spine was borne by a lateral process of the cartilage related to the backward concentration of the originally extensive fin-base. It would appear, therefore, that the spine and the cartilaginous process were developments subsequent, and not prior, to the formation of the pectoral fin; and further, that the spine, instead of being the 'ossified dermal jacket of the entire pectoral appendage', covered only the process of the girdle, and that the fin in at least some cases, such as *Kujdanowiaspis* and *Williamsaspis* (to name both a long- and short-spined form), occurred in a developed and concentrated form behind it. Indeed, it is difficult to believe that any of the arctolepids were without effectively controllable pectoral fins, as Heintz (1938*a*: 23) tentatively and Westoll (1945*b*: 384) more definitely suggest. Assuming, of course, that there were no unknown hydrostatic organs, they would seem thus to have been dynamically incompetent, especially so if they had heterocercal tails, as seems possible. They present a similar sort of problem to that of *Pteraspis* before the caudal region was known, but with different factors. In *Pteraspis* it was possible to predict (White, 1935: 382) the hypocercal tail on the ground that that was the only form which would give an upward and forward thrust to the head (see Grove & Newell, 1936: 289) to counterbalance the depressing effect of the weight of an armoured forebody in a fish-like creature without pectoral fins—otherwise, in fact, *Pteraspis* could never have got off the bottom, for 'the buoyancy and the upward thrust due to the entrance of the rostrum' (Westoll, 1945*a*: 353; Kermack, 1943: 23–27), let alone of the undersurface, would be inoperative once it was grounded on a muddy floor, especially if it rested, as Westoll suggested, 'with the snout somewhat depressed': an even-lobed tail would then as often as not have pushed the snout into the mud, and a heterocercal tail certainly would have done so. The 'typical' arctolepids (that is dolichothoracids) were similarly burdened with a heavily plated forebody as opposed to a lightly protected caudal region, but with the important differences that they had very large pectoral spines, a flat undersurface, and a movable head, and they did not have a hypocercal tail. Doubtless the spines and the undersurface were valuable as gliding-planes when the fish was in motion, but clearly they would be useless in the take-off, especially from soft ground, unless there were means of raising the fore-part, particularly as the pectoral spines sloped forwards and downwards (Heintz, 1935: 238), the effect of which would in itself be to depress the anterior end until that part were raised sufficiently to make the spines horizontal. This raising could be achieved either by the thrust of the tail alone, if hypocercal, as in *Pteraspis*, or by use of an anterior plane inclined upwards, if the tail were even-lobed or heterocercal. Unfortunately there is no direct evidence of the condition of the tail fin in arthrodires except in the brachythoracid *Coccosteus*, in which it is supposed by Heintz (1935*a*: 15, 19, text-fig. 4 (4)) to have been possibly heterocercal —a supposition which is clearly supported by specimens in the British Museum collections, Nos. P.180, P.10798, and especially P.187. This form is adopted for both brachythoracids and arctolepids by Westoll (1945*b*: 384, text-fig. 3). In the absence of evidence to the contrary this premiss as to the tail-form in arctolepids must be accepted for the time being, and it follows that there must have been means of countering the initially depressing effects of both the heterocercal tail and the downward slope of the fin-spines, and since the body lay flat on the bottom when resting, the anterior rising plane must have been provided either by the undersurface of the movable head or by pectoral fins. Westoll (1945*b*: 384–5), although he does not specifically deal with the problem of the take-off, denies the existence of fins in arctolepids, as already noted, and seems to rely on the movement of the head allowed by the cervical joints for 'inducing and controlling pitching'. The up-and-down movement of the head would doubtless be of prime importance in altering elevation in the vertical plane when the fish was water-borne, very much as the dog-fish with amputated pectorals uses the undersurface of its head (Harris, 1936: 491). The tendency of the downwardly inclined pectoral fin-spines and heterocercal tail to put the swimming fish into an uncontrollable, increasingly steep dive could also have been countered by this head movement. Whether the arctolepid with its heavy fore-end and inflexible back could have got off a soft river- or lake-bed by the same device alone seems unlikely, and in spite of the absence of direct evidence as to their presence it would appear to be clear that controllable pectorals were in fact developed.

This view received support in a recent reconstruction of *Phlyctaenaspis* by Denison (1950: 578, pl. iii, fig. 2) based on the form of the plates. Even more convincing is the form of the hinder part of the scapulo-coracoid in various members of the group, including the extreme *Arctolepis* (*Jaekelaspis*) itself, as shown by the 'prespinal lamella' (e.g. Heintz, 1929: pl. vii, pl. xv, fig. 2; 1937: text-figs. 3 C, D), which in outline is similar to that in *Kujdanowiaspis* (Stensiö, 1944: text-fig. 17 B), showing a considerable posterior face along the pectoral embayment. On this evidence pectoral fins may likewise be expected in the arctolepids, although on account of the peculiarities of *Kujdanowiaspis* in the matter of the lost hinge-joint, not necessarily of the same quality. That pectoral fins were standard equipment for the brachythoracids is clear enough from the examples known, and it is most unlikely that the aberrant members of the group, such as *Brachydirus* and the thin Wildungen genera, like *Oxyosteus*, should have discarded such advantageous features. However, owing to the form of the armour the fins must, as Westoll (1945*b*: 385) suggests, have moved backwards, not necessarily on to the flank, but to the level of the AL–AVL suture, where they would have been no more posterior in position relatively than in *Williamsaspis*. The girdle-bearing function of the spinal plate would then be taken over by the two plates mentioned, which in *Williamsaspis* already share it. It would seem even more necessary for *Synauchenia* (Gross, 1932: 45) to have had pectoral fins since the head was completely immobile on the body.

The remarks concerning the necessity for pectoral fins obviously apply to other groups of similar general form, such as the petalichthyids, in spite of the supposed absence of the 'prespinal lamella', which is not necessarily very important, as it might well be that the scapulo-coracoid lacked the perichondrial bone-layer. The presence of pectoral fins would seem to make the derivation of *Gemündina* from *Lunaspis* a little less unlikely (Westoll, 1945*b*: text-fig. 5), but in any case the suggestion that *Pseudopetalichthys* was an intermediate form is most doubtful, for not only is there good reason to suppose that in that genus the whole of the supposed AVL is not the scapulo-coracoid, as Broili first suggested, but its shape in Westoll's figure is wrong, with the fin misplaced and too wide. A fish having such a specialized fin as *Pseudopetalichthys*, with its articular area concentrated to bear only three stout backwardly directed radials, would be a most unlikely lead to the skate-like *Gemündina*.

Finally, before leaving the subject of pectoral fins, it is perhaps worth while to comment on Westoll's (1945*b*: 391, text-fig. 7) suggested derivation of the antiarchan arthropterygian fin from the arctolepid fin-spine. Quite apart from Stensiö's (1944) demonstration of the form of the arctolepid pectoral spine and endoskeletal girdle, the idea that a firmly fixed spine should become loose, acquire a complicated articulation at the base and another half-way along, and break up into a complex series of plates seems to go beyond the widest bounds of probability; in any case, one highly specialized character is not likely to turn into another that is incongruous and equally specialized.

V. THE FORMATION OF THE ARMOUR

Stensiö (1945: 5–6) has given an order of formation of the armour in arthrodires relative to the appearance of the cervical joints. These he considers 'cannot possibly have existed in the ancestors of the arthrodire group, but must be assumed to have arisen very early in the arthrodire group itself'. The force of this statement obviously depends on one's definition of the 'arthrodire group'—and of 'ancestors'. Stensiö suggests that the formation of the exoskeleton of the head and shoulder-girdle—that is, apparently the whole of the body-armour less the median and spinal plates (Stensiö, 1944: 15, 50, 79; 1945: 6)—was accomplished in the primitive gnathostome form from which the arthrodire group was derived before the articulation was formed, and that 'each half of the exoskeletal shoulder was in all probability rigidly attached dorsally (i.e. by the anterior dorsolateral) to the skull-roof'. Subsequently, 'When in early arthrodires the head began to be moveable against the trunk, two halves of the exoskeletal shoulder-girdle were loosened from the dermal skull-roof. In need of a new rigid attachment dorsally they became intimately connected with the scales situated between their dorsal ends, owing to which these scales lost their mobility and fused together into two large median dorsal plates, the anterior median dorsal plate, and the posterior median dorsal plate, which formed the dorsal wall of the exoskeletal shoulder-girdle.'

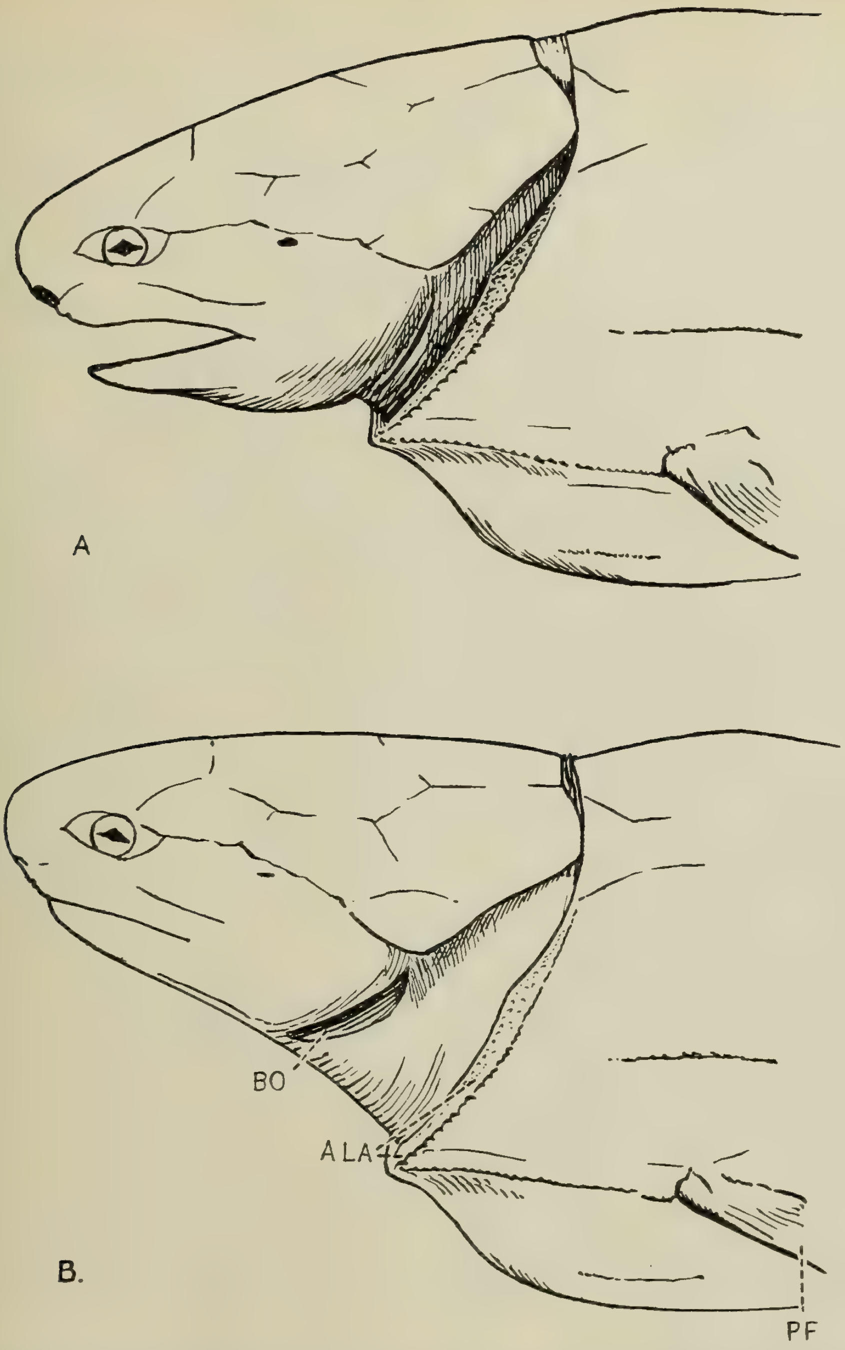
The formation of a movable joint behind a head which was rigidly attached to the body would in itself require a rather complicated series of nicely synchronized adjustments. In such a case the loosening of the head from the shoulder-girdle must surely have taken place *pari passu* with the development of the internal articulation and the modification of the musculature, if not before, since some degree of movement would appear to be a prerequisite of its formation. Moreover, so as to allow such movement without damage, there must also have been at least a partial development of the exoskeletal articulation.

However, this development becomes still further involved by the supposition that to meet the loss of rigidity caused by the loosening of the head from the shoulder-girdle, the dorsal scales fused together to form two large median dorsal plates.

The formation at this stage of the exoskeletal articulation would be interesting because it might indicate the point at which the euarthrodires and the antiarchs separated, for the articulations are reversed in the two groups, the trochleae being on the body-armour and the fossae on the head-shield in the euarthrodires, and vice versa in the antiarchs.

As an alternative to this complex sequence of events, we may suppose that the internal shoulder-girdle, the scapulo-coracoid, was primarily horizontal, supporting the primitive horizontal pectoral fin formed from the lateral fin-fold, and that it remained so in the arthrodires, the scapular process being a subsequent development related to the concentration of the radials and the formation of a controllable pectoral fin. The original exoskeletal support of the shoulder-girdle was therefore formed by the interlateral and possibly the spinal plates, and the attachment to the anterior laterals, apart from a possible marginal selvage (which may have also occurred along the top of the anterior ventrolaterals), followed later with the development of the scapular process.

Again, in the suggested sequence of development of the cervical joints and armour noted above, it would seem possible that the internal articulation was developed before the formation of the plate-armour (and with it the external articulation), and that the ancestors of the arthrodires proper and the antiarchs separated at some point between these two developments, i.e. after the formation of the internal articulation and before that of the armour and external articulation. The latter was surely developed in all lines, and its absence, as in some arctolepids (e.g. *Kujdanowiaspis*, *Euryaspis*), the petalichthyids, &c., is a secondary feature. Westoll (1945*b*: 385) has suggested that the cervical articulation was 'initially a functional adaptation'—it only allowed 'relative movement about a transverse axis, and it would therefore have prevented lateral movements which might induce uncontrollable yawing movements. The up-and-down movement of the head may have been of positive value in inducing and controlling pitching.' It is difficult to believe that yawing (i.e. deviation in the horizontal plane from the intended route) was of much significance in the lives of the early arthrodires, bottom-haunting and poor swimmers that they must have been, or even if it were, that inability to turn the head sideways would have checked it. On the contrary, in view of the importance of lateral head-movements in changing direction (Gray, 1933), the fixity of the head and body in the vertical plane might well have been disadvantageous in correcting involuntary lateral movements. The second suggestion that the articulated head was a means of altering level while swimming seems much more likely and would have been of especial advantage to the ancestral arthrodires before the pectoral fins became more controllable by concentration, particularly if they had heterocercal tails. However, it is possible that this was originally connected with breathing, the movement of the head facilitating this function by a kind of bellows-action. Indeed, if the gill-opening was placed where Stensiö (1944: text-fig. 14) has pictured it—and it could hardly have been very differently placed, unless perhaps a little lower down—movement of the head was apparently essential in some form to allow the slit to open. Moreover, there may, too, have been some connexion between the position of the gill-slit and the neck-construction as shown by the apron described below (p. 292), since the 'pocket' so formed would allow the opening to come farther in and behind the head, where it could open more widely with a smaller movement of the head (Text-fig. 38). If there was a relation between the movements of the head and breathing it is difficult to understand why the articulation ever disappeared, as it undoubtedly did, and what is more, quite early in the history of the group: it had already gone except for overlapping flanges in the Lower Old Red arctolepids *Euryaspis* (Bryant, 1934: 137) and *Kujdanowiaspis* (Stensiö, 1944: text-fig. 17*A*); while the movement of the head must have very nearly ceased, among the brachythoracids, with the development of the extrascapular plates in the Middle Old Red *Coccosteus minor* (Heintz, 1938*a*: text-fig. 2 (1); Stensiö, 1945: text-fig. 12 A; shown also in *C. decipiens* by Gross, 1940:



Text-fig. 38. Reconstruction of the head and shoulders of an arctolepid arthrodire (*Williamsaspis*), showing the supposed constriction of the neck and movement of the head in breathing. A. Inhalant position. B. Exhalant position. (For explanation of lettering see pp. 303–304.)

text-fig. 14*c*), and completely in the fused head and body-armour of the Upper Devonian *Synauchenia* (Gross, 1932: text-fig. 25).

It is conceivable that in these cases the gill-slit moved downwards into a more chimaeroid-like position where it would open directly below without the need of head-movement—or at any rate into a sort of vestibule formed from the remnant of the neck-pocket.

VI. THE APRON

Structures similar to the apron of the anterior lateral plate in *Williamsaspis* have been described in a number of arthrodires in differing degrees of development and with varying composition (Text-fig. 19). What Heintz considers the 'original' condition (1929: text-figs. 8, 9, 11, 13, &c.; 1934*a*: 137) is shown by such Lower Devonian arctolepids as '*Jaekelaspis*' in which the low apron is formed by the interlateral plate without part of the anterior lateral plate being turned inwards, a feature which is seen apparently in a fairly early stage in *Kujdanowiaspis* (Stensiö, 1944: 27, text-fig. 17A). Then follows the condition seen in *Phlyctaenaspis* (Heintz, 1934*a*: 138, text-figs. 3–5), the inturned front quadrant of the anterior lateral being more clearly marked, and from this point Heintz (1931*b*: 237, text-fig. 10; 1938*a*: 24, text-fig. 7) derives a morphological series *Coccosteus*, *Dinichthys*, *Titanichthys*, *Heterostius*. It is clear that there were other types of development which involved the expansion of the anterior lateral part of the apron, as in the curious Downtonian form *Palaeacanthaspis* (Stensiö, 1944: 26, text-figs. 3, 4), the Upper and Middle Devonian ptyctodonts *Rhamphodontus* and *Rhamphodopsis* (Watson, 1934: 455, text-figs. 6, 7; 1938: 402, text-fig. 3); *Gemündina* (Watson, 1937: 138, text-fig. 25), and of course *Williamsaspis*.[1] All these formed the apron chiefly from the anterior lateral, especially *Williamsaspis*, in which the interlateral does not seem to have taken part at all, although the anterior dorsolateral did so substantially. The development of this peculiar feature to such a degree in such widely divergent forms is of no little interest, both from the systematic and the functional standpoint. What was the precise function of the apron is not clear. The obvious explanation is that it formed the hinder wall of the gill-chamber (Watson, 1938: 402) comparable to that formed by the shoulder-girdle in fishes generally, but there are differences. In the latter case the internal lamina is smooth and clearly marked off from the external part of the dermal shoulder-girdle; whereas in the arthrodires the apron is a direct modification of the dermal armour still bearing external ornamentation and doubtless covered by epidermis. In *Rhamphodopsis* the ornamentation appears to be similar to that of the external bones generally but lighter and fading out mesially, but in *Rhamphodontus* it is formed of peculiar, linearly arranged tubercles on the lower part only, while *Palaeacanthaspis* had a special triangular pyramidal ornamentation (Stensiö, 1944: 69, pl. vi, fig. 3; pl. ix, fig. 2; text-figs. 3, 7*a*), similar to that in *Williamsaspis* and differing only in that the tubercles are quite smooth and point backwards instead of forwards.[2] It is only in *Gemündina*, in Watson's (1937: text-fig. 25A) restoration, that the apron is smooth and recessed in the manner to be expected of a true branchial wall.

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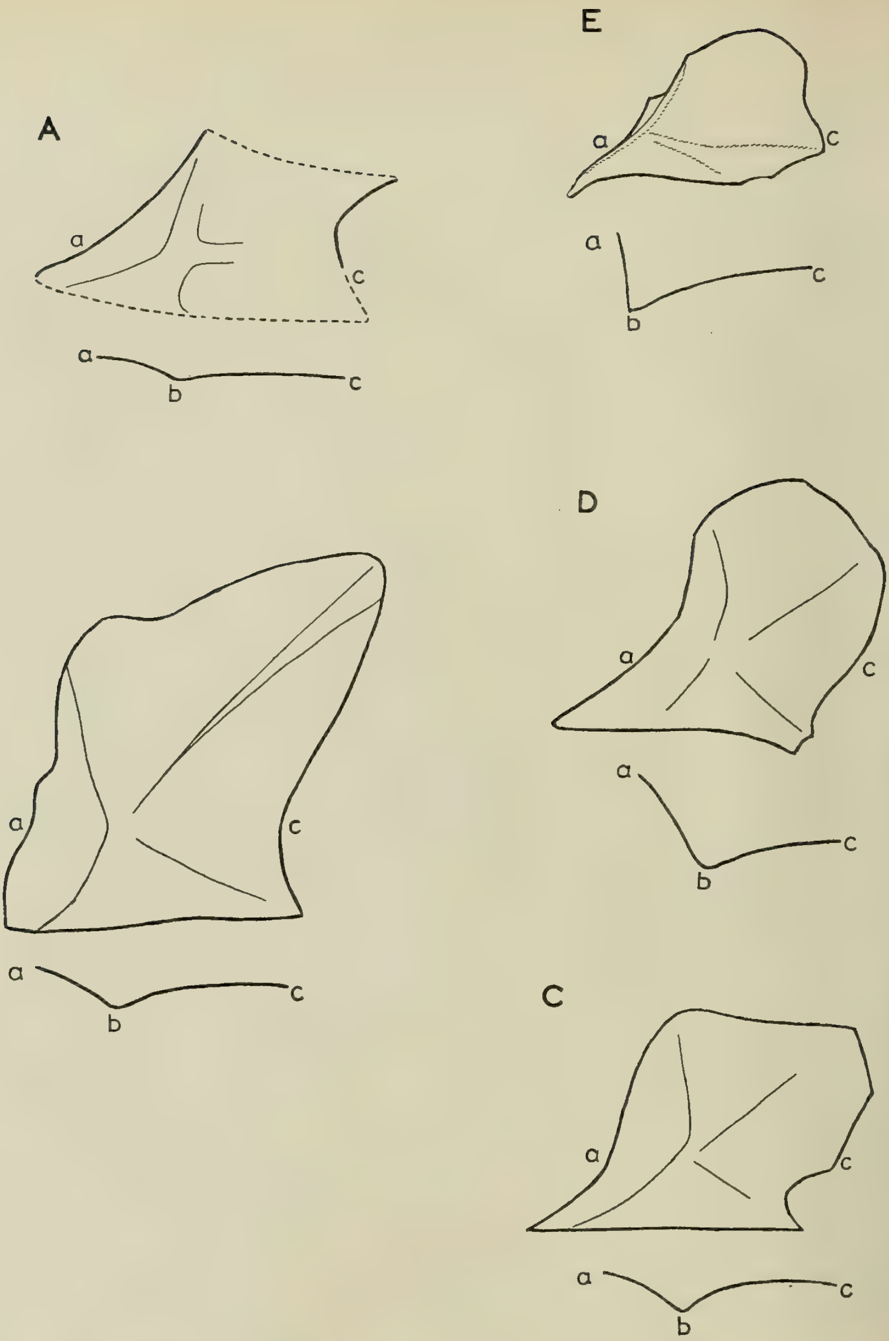
[1] It would appear from Gross's sketch (1932: 27, text-fig. 11) that the apron was moderately well developed at least in *Hadrosteus* among the Wildungen brachythoracid arthrodires.

[2] The ornamentation on the interlateral in *Dinichthys* which, according to Heintz (1932: 176), is the

It is difficult to see what use this ornament had, if the apron had formed the back of the gill-chamber and was covered in soft tissue, for it is very little raised above the surface of the bone, and indeed the fact that it faces different ways in different genera suggests that it was just ornament and had no other function. Moreover, it seems unlikely that such ornamentation would persist after the surface had become functionally an internal structure. One is tempted to suppose that in fact it was not internal and that the apron did not form the back wall of the gill-chamber, but that the flexible-throat or half-neck, which all arthrodires with movable heads must have had, in these forms with ornamented aprons, narrowed rapidly backwards and inwards from the jaws to the grooved mesial edge of the apron which is, as Heintz's series shows, the morphological front margin of the plates from which it was formed. It is quite clear that this was the case in such intermediate forms as *Phlyctaenaspis* and *Kujdanowiaspis* where the partly inturned front segment of the anterior lateral plate was still obviously part of the external surface and could not have functioned as the hinder wall of the gill-chamber (Text-fig. 39). The form of the mesial margin seems to support this idea, for the rising groove would appear to be due to the increase in thickness of the free integument.

In spite of a superficial resemblance, the arthrodire apron is quite different from the '*crista transversalis interna anterior*' of the antiarchs (Stensiö, 1931: 80, text-fig. 35; Gross, 1933*b*: 17, pl. 3, fig. 1, text-fig. 4A; Stensiö, 1948: 108, &c.) in both origin and function. The *crista* is an internal structure without ornament, formed by laminar processes from the inner surface of the bones, and bears the articular fossae; it is neither homologous nor analogous with the apron. Unless there was a connexion with breathing, as suggested above, the neck constriction and where developed, the apron, would seem to have more drawbacks than advantages. The area provided by the inner face of the apron would, of course, afford good anchorage for the body muscles, but the need for this is not obvious in a well-corseted form like *Williamsaspis*, although possibly more marked in those with contracted body-armour. On the other hand, the pocket between the back of the gill-chamber and the front of the apron seems a likely harbour for parasites, such as barnacles (Clarke, 1921: 62) and dirt, and during movement forwards with the head raised the pocket on each side would tend to impede progress, though not necessarily seriously in a slow-moving animal with well-developed pectoral fins. However, it seems to have had no markedly negative survival value. The occurrence of the apron among the arthrodires is peculiar, for the time spans almost the whole Devonian and the genera in which it is best developed are certainly not close relatives. As remarked before, all the arthrodires with a workable articulation between the head and body-armour must have had a soft neck to allow the upward movement of the head, and all may have had the constricted neck, but very few had a large apron, so that its development is not necessarily connected with that arthrodiran peculiarity. Nor does it seem connected with the habits in so far as one may deduce such matters from

only part of the armour in this genus to be ornamented, is seen in P.9395 to consist of fine tubercles with a triangular worn surface and the apex directed forwards.



TEXT-FIG. 39. Sketches of left anterior lateral plates forming a morphological series to show development of the apron from the anterior quadrant of plate. A. *Arctolepis* [*Jaekelaspis*]. After Heintz, 1929. B. *Phlyctaenaspis*. After Heintz, 1934*a*. C. *Kujdanowiaspis*. After Stensiö, 1944. D. *Palaeacanthaspis*. After Stensiö, 1944. E. *Williamsaspis*. *a–c*, sections through growth-centre of plate, *b*. (All drawn so that length of section is constant.)

external form. The ptyctodonts had a wide, flat undersurface with large pectoral fin-spines in the same plane, and were presumably bottom-dwellers in fresh waters; *Williamsaspis* had a rounded undersurface (Text-fig. 12) with high pectoral keels and was probably an active marine swimmer, while *Palaeacanthaspis* with its flat bottom but smaller and somewhat raised pectoral fin-spines held an intermediate position. In fact the apron is the chief common factor between them, but we may note that all three seem to have been arctolepid derivatives. On the other hand, *Gemündina*, which stands apart by reason of its extreme specialization and the smooth recessed apron that may in fact have functioned as the wall of the branchial cavity, is for other reasons considered to be related to the brachythoracids.

VII. RELATIONSHIPS

During the last two decades very much information has come to hand concerning the arthrodires and their allies, mostly in the works of Heintz, Broili, Gross, and Watson, and from the numerous classical memoirs of Stensiö we have details of their internal structure far beyond our expectations. But as has often been pointed out, there is always the difficulty of separating characters due to relationship from those due to function, a difficulty that is particularly marked in extinct groups owing to the imperfect nature of our information and further confused by conflicting theories.

At the start we may accept Stensiö's (1944: 75; 1948: 222) view that the group 'Arthrodira' includes in it, as having a discernible common origin, not only the typical arthrodires, the Brachythoraci and the Arctolepida (Dolichothoraci), but all the oddly specialized groups variously associated with them—Acanthothoraci, Petalichthyida, Stegoselachii, Phyllolepida, Ptyctodontida, Rhenanida, and Antiarchi. All these may be expected to have a common ground-plan in internal structure which may or may not be masked in part externally by their particular specializations, yet still show in some simple functionally unimportant characters their proper relations one to another.[1]

The most obvious cleavage comes between the antiarchs and all the remainder. Westoll (1945*b*: 391) and Stensiö (1948: 147, 221–2, 613) both seem to derive this curious group directly from already armoured arthrodires, but this, as I have already suggested, I believe unlikely. The basic difficulty of the development of the antiarch arthropterygium seems under-estimated: Westoll postulates the development of articulations in the arctolepid spine: Stensiö (1944: 67) derives it from a fin such as he believes *Palaeacanthaspis* had and states that 'one may even suspect that the concentration had proceeded so far that the endoskeleton as a whole was of a mesorhachic ("archipterygial") type'. But apart from the unlikelihood of the development of articulations in a spine, Westoll's theory is based on a misunderstanding of the nature of the 'prespinal lamella'. Nor can I believe that the arthropterygium could be developed readily from a concentrated arthrodire fin as Stensiö (1948: 222) supposes, even were the mesorhachic nature of the acanthothoracid fin proved, which it is not—and no arthrodire is known with such a fin.

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[1] That 'the taxonomic significance of a character varies inversely as its functional value' is a principle of systematics which, if not always true, is always worth bearing in mind.

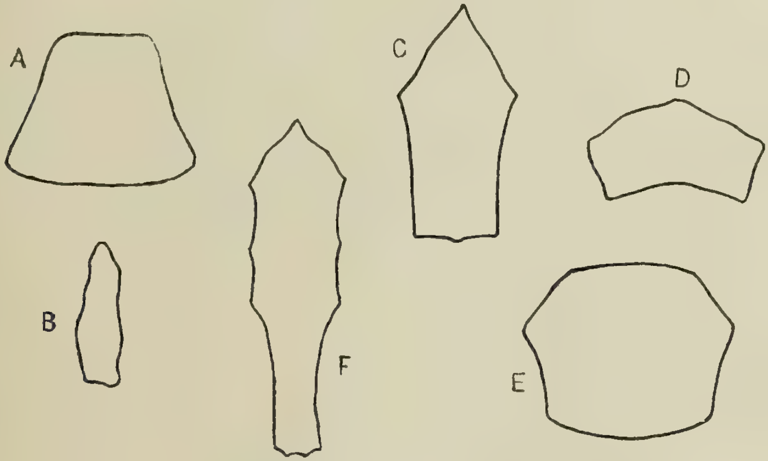
The general similarity between the armour of the antiarchs and that of the arctolepid arthrodires seems to me somewhat misleading, for the differences generally glossed over are important. Stensiö (1948: 189–211, 612) has made a profound comparison between the plates of the antiarchs and arthrodires, yet major difficulties remain unsolved even allowing for the distortions due to the specialization of the head and pectoral fins in the former group. Such 'soft' details as the sensory canals are fundamentally the same, as would be expected from common origin, but the patterns of the armour are no nearer to one another in detail than might be expected in independent development in related but already separated groups. The reversing of the ball-and-socket of the external articulations seems a clear indication of this independence, for the reversal in the antiarchs, were they developed from already armoured arthrodires, would be a complicated change without obvious benefit. As I see it the antiarchs developed from ancestral arthrodires before the development of the plate-armour.

Stensiö (1944) has shown the brachythoracids to be more primitive than the dolichothoracids in respect of their pectoral fins, but as mentioned above, they are more specialized in respect of their reduced body-armour. There can be little doubt that these two groups represent the two main branches of arthrodires from which all the other related groups, except the antiarchs, have been derived, and their common ancestor had the long-based fin of the brachythoracids and the long body-armour of the dolichothoracids. But the precise relationships of the other groups to them are not so easy to determine. These two groups are most obviously separated the one from the other on the length of the body-armour, but it is a character of functional importance and, although reduction in the brachythoracids is universal, it certainly could also have happened in the dolichothoracids—and did.

Stensiö (1944), in his important work on the acanthothoracids, has compared their specializations, particularly the short body-armour and the pectoral fin-bases, with the characters of all the other groups. He concludes (1944: 77) that although most nearly allied to the dolichothoracids they 'are to a certain extent intermediate in character between the *Dolichothoraci* (*Acanthaspida*) on the one hand and the *Petalichthyida*, *Stegoselachii*, *Phyllolepida*, and *Ptyctodontida* on the other', and 'it has appeared that the differences between the *Dolichothoraci* (*Acanthaspida*) and the Brachythoraci are greater than what has been assumed hitherto'. Yet the neurocranium of *Buchanosteus* has shown yet one more fundamental similarity between the two main groups, while some of the resemblances noted between the acanthothoracids and the others named seem to be due to functional convergence, particularly in respect of the pectoral armour and fin. Nevertheless, all these groups must undoubtedly, as Stensiö says (1944: 77), 'be more closely allied to each other than has been believed by several previous writers' and some even more closely than Stensiö has suggested: for example, the acanthothoraceids are simply arctolepids specialized by the shortening, with the loss of some plates, of the body-armour and of the pectoral fin-base, and should be placed in a sub-group of the arctolepids.

The williamsosteids are also undoubtedly arctolepids and their pectoral fin-base and the unproduced spinal plate may show a more original type than the dolichothoracids with their enormous spines. In other words, *Williamsaspis* is possibly a progenomorph,[1] that is, the little-modified survivor of the ancestral stock from which the more specialized forms, such as the dolichothoracids, were derived, although it may have suffered some reduction in the development of a spinal process.

The relationships of the other odd groups have not yet been clearly determined. Stensiö (1942: 23–25; 1944: 75; 1948: 222) places them all as equal orders in the Euarthrodira, although Westoll (1945*b*: 386, text-fig. 5) has attempted to link the rhenanids to the petalichthyids through the stegoselachian *Pseudopetalichthys*, as noted above. But a hint of affinities is given by one curious and otherwise possibly unimportant feature—the shape of the nuchal plate (Text-fig. 40). In all the brachythoracids this plate is widest behind, narrowing forwards, a feature shared only by the diminutive plate of the rhenanid *Asterosteus* (Stensiö, 1948: 194, text-fig. 69), and the rhenanids may be an early offshoot from early brachythoracids—at any rate they would come more readily from forms with a long fin-base than from petalichthyids.



TEXT-FIG. 40. Nuchal plates of the Euarthrodira, (*a*) a brachythoracid, (*b*) a rhenanid, (*c*) an arctolepid, (*d*) a ptyctodont, (*e*) a phyllolepid, (*f*) a petalichthyid. (After Heintz, Stensiö, Gross and Watson. Various scales.)

All the other groups have the nuchal narrowing behind as in the dolichothoracids. This is most marked in petalichthyids which may have developed from arctolepid stock by the inwards and backwards migration of the orbits (Stensiö, 1948: 199, text-fig. 72). The phyllolepids (Stensiö, 1936: text-fig. 9) may have developed from the same group by the alteration in proportion of most plates, particularly by the lateral expansion of the nuchal plate and its fusion with the centrals, and the suppression of others in front. The ptyctodonts seem to have become specialized in the skull-roof by similar processes working in a different direction (Watson, 1938: text-fig. 2). All these groups, incidentally, carried well-developed pectoral spines.

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[1] A typical progenomorph is the chordate *Jamoytius* (White, 1946) which has preserved the characters of the almost ideal vertebrate ancestor, lateral and median fin-folds, &c., until the Upper Silurian.

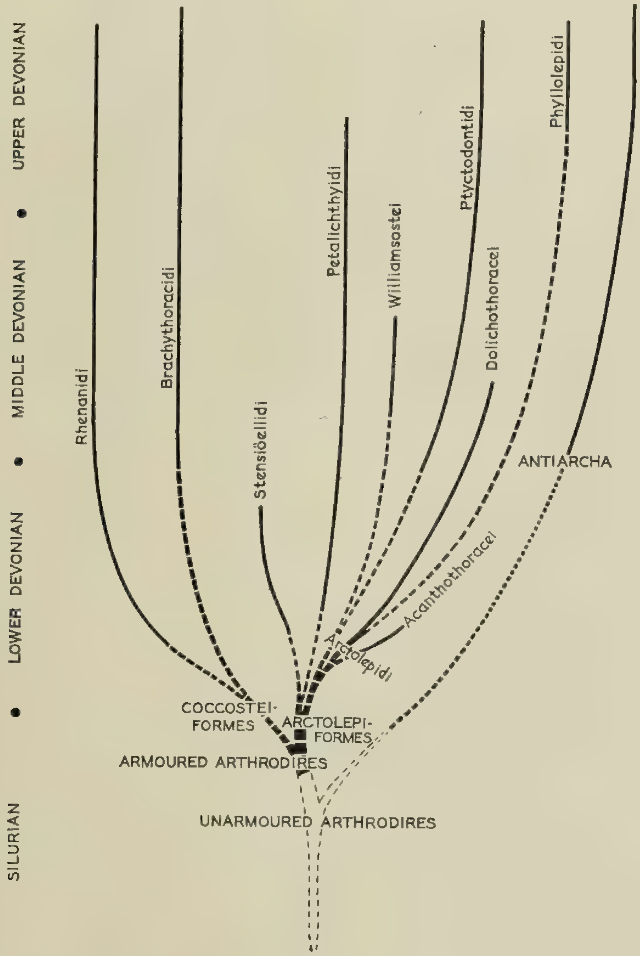
There remains only the Stegoselachii, a 'group' which is just a systematic dust-bin for arthrodires of uncertain position (Stensiö, 1942: 25). *Nessariostoma* and *Cratoselache*, the last of the arthrodires, are insufficiently known even for guessing their relationships, except for saying they have nothing to do with one another. *Pseudopetalichthys* and *Stensiöella* (Broili, 1933 *a*, *b*) seem to me possibly to be differently preserved versions of the same or a closely related animal in spite of the obvious discrepancies in the published interpretations of their structure, but without the opportunity of examining both specimens this is mere surmise. Broili's reference of both these forms to the petalichthyids may after all be not so far from the truth—they do not resemble any other group more than they do the petalichthyids, although the likeness there seems rather faint. On the published evidence I can see no reason for questioning Broili's (1933*b*: text-fig. 5) original interpretation of the shoulder-girdle of *Pseudopetalichthys* (see also Stensiö, 1944: text-fig. 18; Westoll, 1945*b*: text-fig. 5*c*), but if this is approximately correct, neither *Pseudopetalichthys* nor *Stensiöella* appears likely to have been derived from such forms as the contemporary *Lunaspis*, although they may represent the older less specialized stock.

Text-fig. 41 represents my present views on the relationships of the arthrodires to one another and may be expressed as follows:

Class ARTHRODIRA
 Division A. Euarthrodira
  Order 1. Arctolepiformes
   Sub-order a. Arctolepidi
    Super-family i. Williamsostei
    Super-family ii. Dolichothoracei
    Super-family iii. Acanthothoracei
     iv. (Ancestral ptyctodonts)
     v. (Ancestral phyllolepids)
   Sub-order b. Ptyctodontidi
   Sub-order c. Phyllolepidi
   Sub-order d. Petalichthyidi
   Sub-order e. Stensiöellidi
  Order 2. Coccosteiformes
   Sub-order a. Brachythoracidi
   Sub-order b. Rhenanidi
 Division B. Antiarcha

This classification differs considerably from most of those recently published (Gross, 1937: 50; Watson, 1937: 143; Moy-Thomas, 1939: 124; Berg, 1940: 365; Romer, 1945: 574–5; Westoll, 1945*b*: 394), except that of Stensiö (1944: 75; 1948: 222), who first demonstrated the relationships between the various sub-orders grouped above in the order Arctolepiformes. It does, however, differ somewhat in emphasis from Stensiö's arrangement and is based on different argument.

Such a classification may be criticized for the reason that the stratigraphical background has been ignored in that the known times of the first appearance of the various groups are not in keeping with the supposed derivations, and this is to some extent true. But there are no certain connecting links between any of the groups, all of which are by the known records discrete; our knowledge is hopelessly inadequate in any case, and the length of the supposed missing chain is not a matter to outweigh arguments based on known form.


UPPER DEVONIAN
MIDDLE DEVONIAN
LOWER DEVONIAN
SILURIAN
Rhenanidi
Brachythoracidi
Stensiöellidi
Petalichthyidi
Williamsostei
Ptyctodontidi
Dolichothoracei
Phyllolepidi
ANTIARCHA
Acanthothoracei
Arctolepidi
COCCOSTEI-FORMES
ARCTOLEPI-FORMES
ARMOURED ARTHRODIRES
UNARMOURED ARTHRODIRES

TEXT-FIG. 41. Suggested relationships of the arthrodires.

There remains to me only the pleasant duty of expressing my thanks to those from whom I have received assistance. Firstly my thanks are due to Mr. W. E. Williams, the discoverer of the fossils, who gave them to the British Museum (Natural History), and then to Mr. R. Bedford for the active part he played in bringing them to my notice, while Mr. C. St. J. Mulholland, Government Geologist of New South Wales, kindly allowed me to examine the unique specimen of *Notopetalichthys*. Mr. H. A. Toombs,

as always, has been my right hand, and to him much praise is due for his skill in developing the specimens.

To my friends, Professor Erik Stensiö and Professor Stanley Westoll I am indebted for helpful and stimulating discussions, even though our conclusions have not always coincided.

Finally, I have to thank Mr. R. Baker and Mr. F. M. Wonnacott for assistance in the preparation of the manuscript.

Since this paper was written I have again had the very great pleasure of visiting the Paleozoological Department of the Swedish Museum of Natural History, Stockholm, where Professor E. A. Stensiö most generously placed at my disposal the whole of his superb preparations of arthrodire material and the typescripts of four monumental works relating to them, in which the shoulder-girdles of at least a dozen Wildungen genera are described. It is difficult adequately to express my indebtedness to Professor Stensiö for his generosity and kindness.

Later I travelled to Oslo, where I enjoyed the hospitality of Professor Anatol Heintz at home and in the Paleontological Museum, and availed myself of my friend's wide knowledge of the group. My warmest thanks are due to both Professor and Mrs. Heintz for their kindness.

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LETTERING USED IN TEXT-FIGURES

AbA	Attachment area of abductor muscles.
AbM	,, ,, ,,
AbP	,, ,, ,,
AdA	Attachment area of adductor muscles.
ADL	Anterior dorsolateral plate.
AdM	Attachment area of adductor muscles.
AdP	,, ,, ,,
AL	Anterior lateral plate.
AL″	Internal impression of anterior lateral plate.
ALA	Apron of anterior lateral plate.
ALA(L)	Apron of left anterior lateral plate.
AMA	Anterior mesial angle of coracoid.
AMV	Anterior median ventral plate.
APo	Anterior postorbital process.
AR	Articular facet for anterior ? fin-ray.
Ar	Broken base of articular surface.
AVL	Anterior ventrolateral plate.
BE	Undersurface of neurocranium.
BO	Branchial opening.
CE	Central plate.
COA	Area of overlap on to central plate.
csg	Central sensory groove.
Cv	Cavum cerebrale cranii.
C+N	Centronuchal plate.
DE	External opening of ductus endolymphaticus.
Fl	Mesial flange.
FSO	Fin socket.
Gl–Gl	Articular area for radials.
Gr	Groove on mesial edge of apron.
IL	Interlateral plate.
ILi	Inner perichondrial bone of interlateral plate.
IL(L)	Left interlateral plate.
ioc	Infraorbital groove.
JV	Vein draining into jugular vein from ventral surface.
lc	Main lateral line groove.
MA	Marginal plate.
MC	Median cusp.
MD	Median dorsal plate.
MOA	Area of overlap on to marginal plate.
mp	Median pit-line groove.
MSP	Mesial process of posterior superognathal.
N	Branches of 10th nerve.
N′	Exit of branches of 10th nerve.
NOA	Area overlapped by nuchal plate.
NU	Nuchal plate.
OLA	Overlapping area of anterior lateral plate on anterior dorsolateral plate.
OLP	Overlapping area of posterior lateral plate on posterior dorsolateral plate.
OM	Orbital margin.
Or	Inner wall of orbit.

ORB	Orbit.
PAN	Paranuchal plate.
PDL	Posterior dorsolateral plate.
PF	Pectoral fin.
Pi	Pineal plate.
PL	Posterior lateral plate.
PM	Postmarginal plate.
PmOA	Area of overlap on to postmarginal plate.
PMV	Posterior median ventral plate.
poc	Preopercular groove.
pp	Posterior pit-line groove.
PPo	Posterior postorbital process.
PRO	Preorbital plate.
PTO	Postorbital plate.
PVL	Posterior ventrolateral plate.
R	Rostral plate.
Sc. 1–5	Scars.
Sc Co	Scapulo-coracoid cartilage.
SHy	Hyoid vein.
SO	Pectoral fenestra.
soc	Suborbital groove.
SP	Spinal plate.
SS	Suborbital shelf.
SV	Supravagal process.
VC	Vascular canals.
VJu	Jugular vein.
VJu′	Exit of jugular vein.

PLATE 26

Williamsaspis bedfordi gen. et sp. nov.

FIG. 1. Ventral view of carapace. The holotype, P.27073, × 1½. (For explanation see Text-fig. 3.)

FIG. 2. Left side view of same, lit from below. × 1½. (For explanation see Text-fig. 7.)

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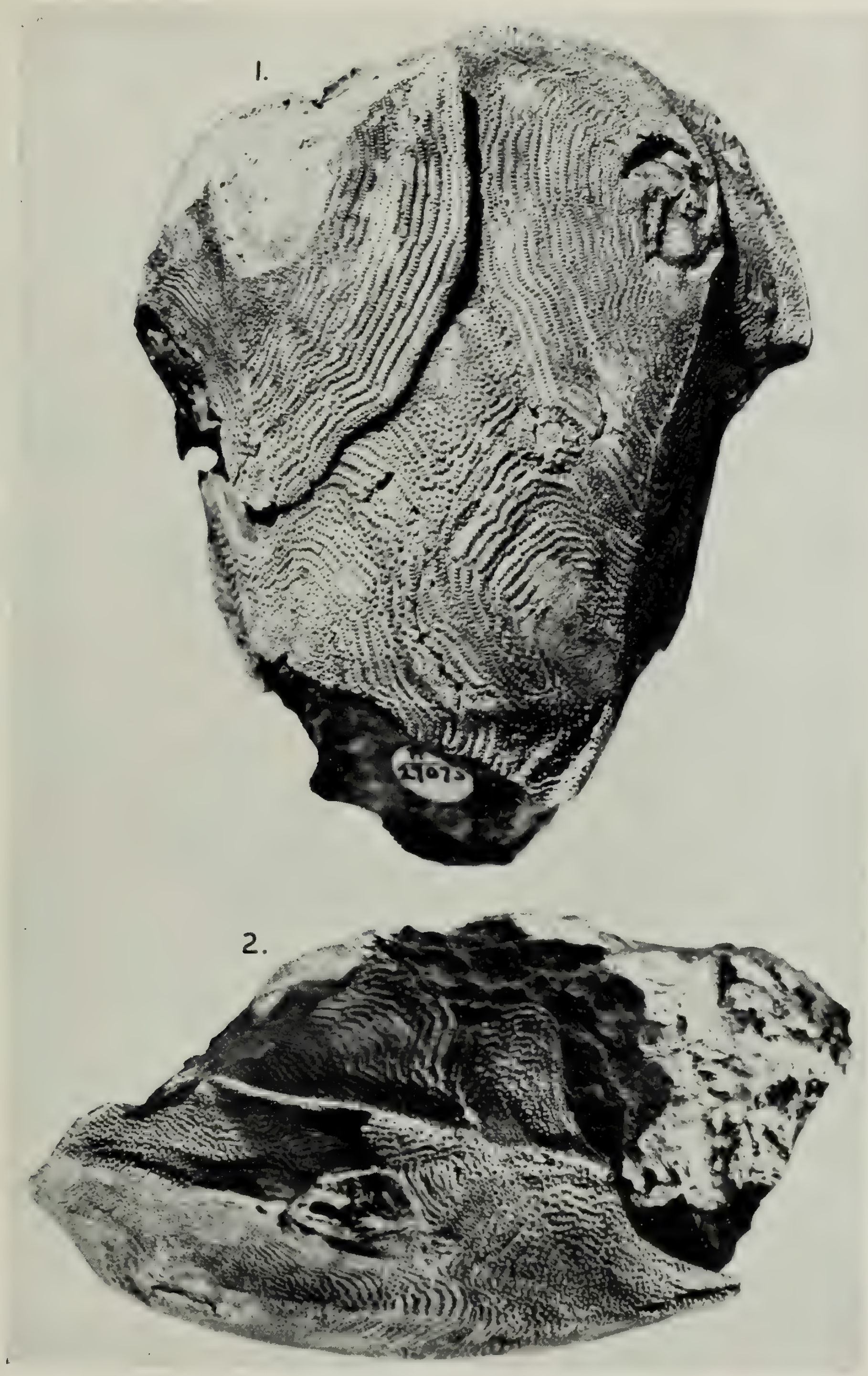


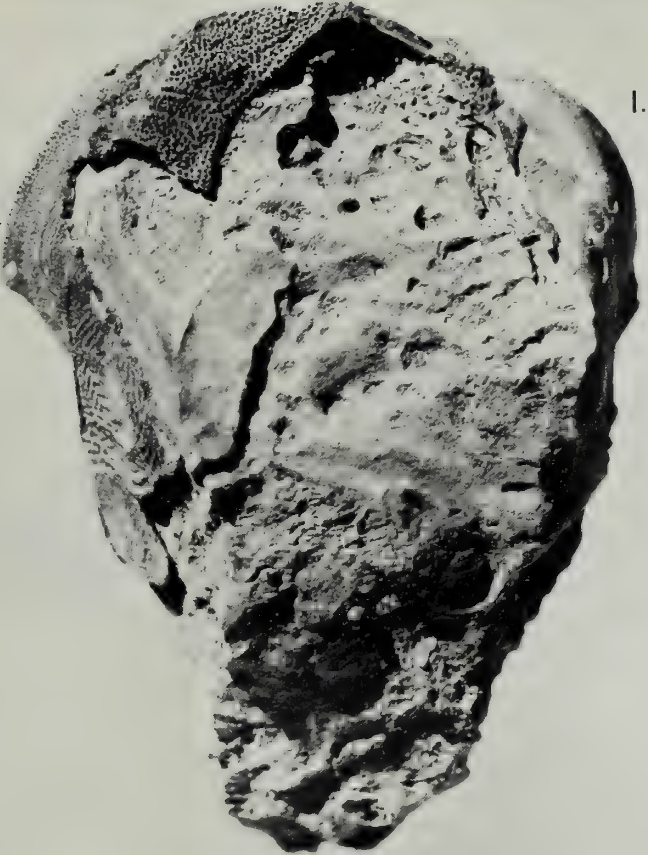
WILLIAMSASPIS BEDFORDI

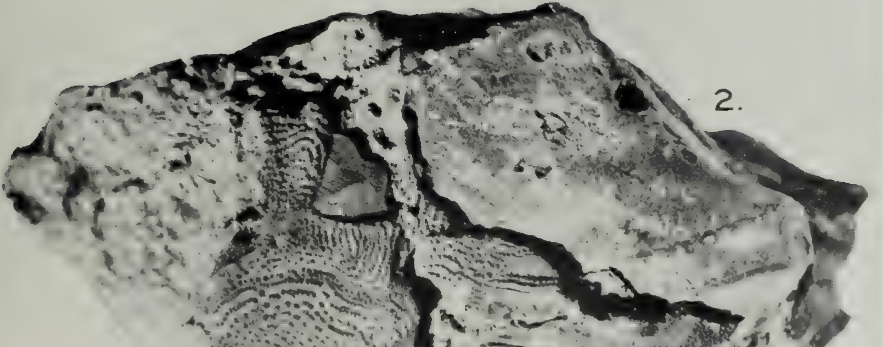
PLATE 27

Williamsaspis bedfordi gen. et sp. nov.

Fig. 1. Antero-dorsal view of carapace, approx. at right-angles to the anterior lateral apron. The holotype, P.27073, ×1½ approx. (For explanation see Text-fig. 5.)

Fig. 2. Right side view of same, × 1½ approx. (For explanation see Text-fig. 4.)





WILLIAMSASPIS BEDFORDI

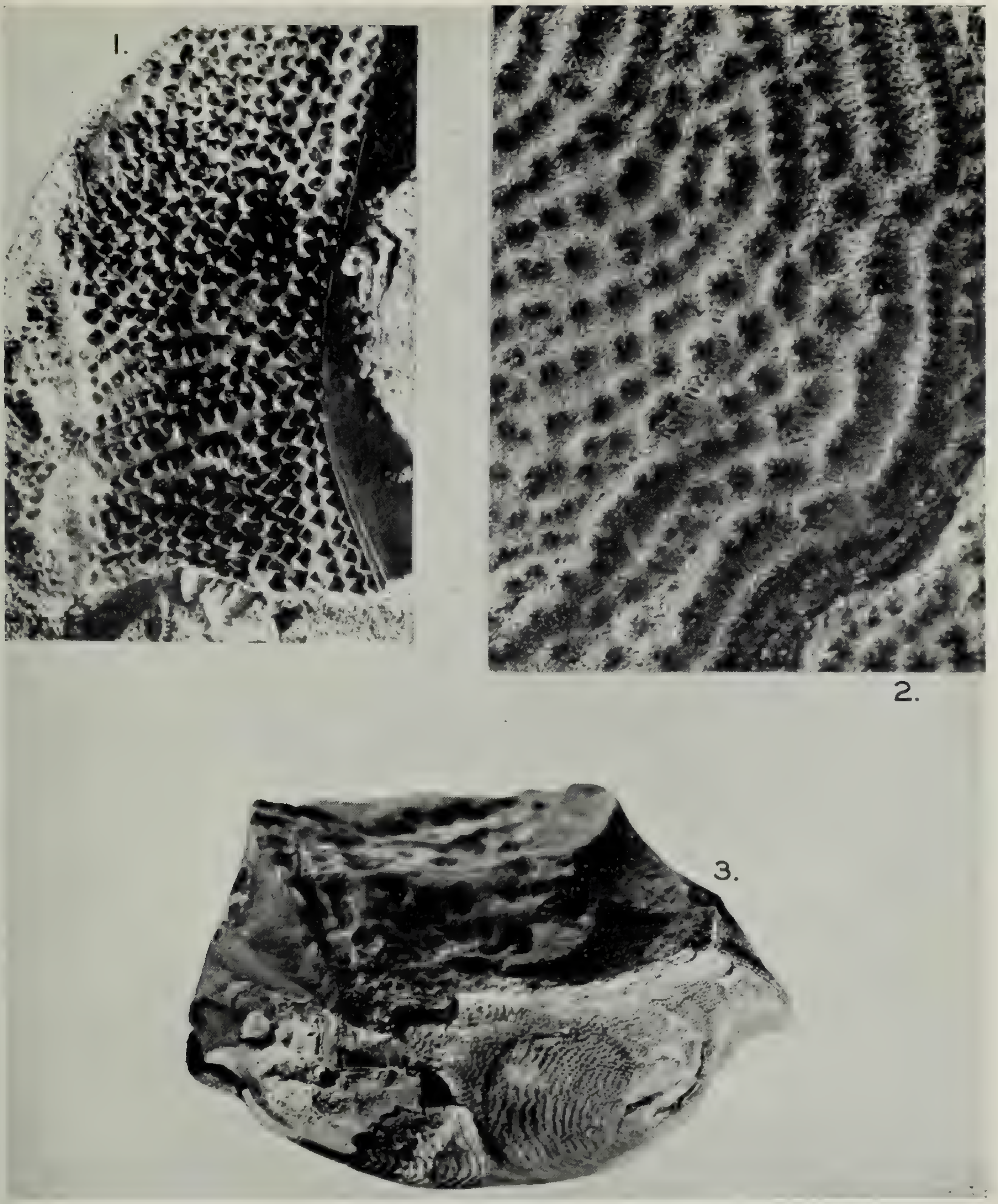
PLATE 28

Williamsaspis bedfordi gen. et sp. nov.

FIG. 1. Ornamentation on anterior lateral apron. The holotype, P.27073, ×4½. The grooved mesial margin is retouched.

FIG. 2. Ornamentation on right posterior ventrolateral plate at margin with posterior lateral. Top to right. The holotype, ×7.

FIG. 3. Carapace in front view, slightly uplifted and lit from below. The holotype, ×1½ approx. (For explanation see Text-fig. 6.)



WILLIAMSASPIS BEDFORDI

PLATE 29

Williamsaspis bedfordi gen. et sp. nov.

FIG. 1. Area of right pectoral socket. The holotype, P.27073, ×4½. (For explanation see Text-figs. 16, 17.)

FIG. 2. Area of left pectoral socket, lit from below. The holotype, ×4½. (For explanation see Text-figs. 16, 19.)

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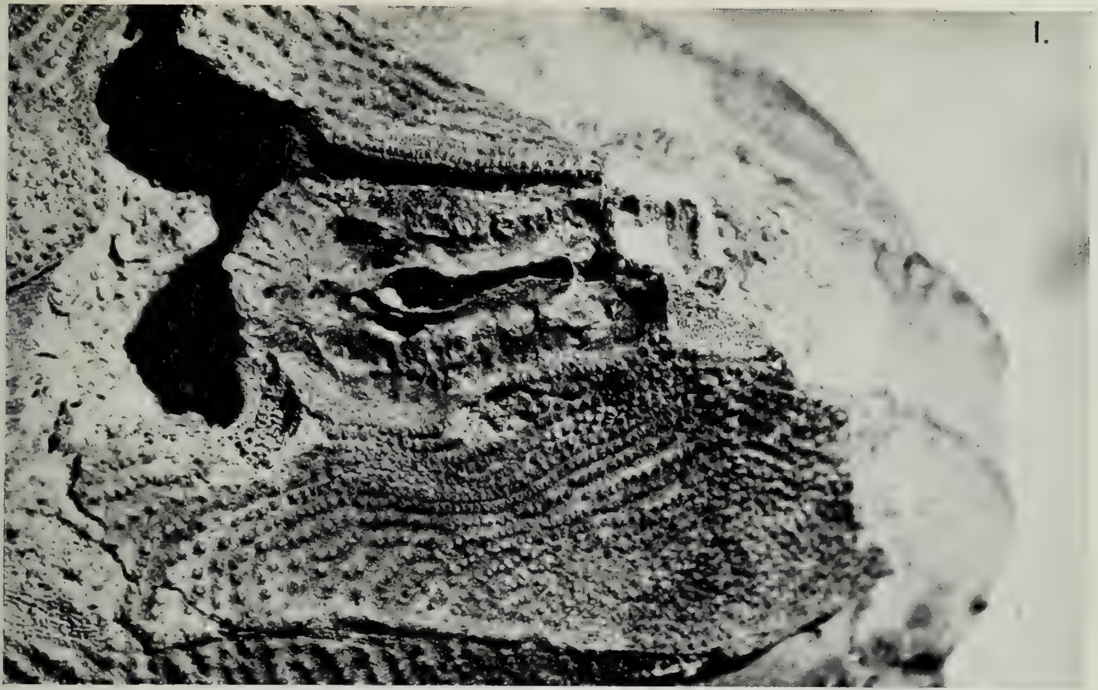

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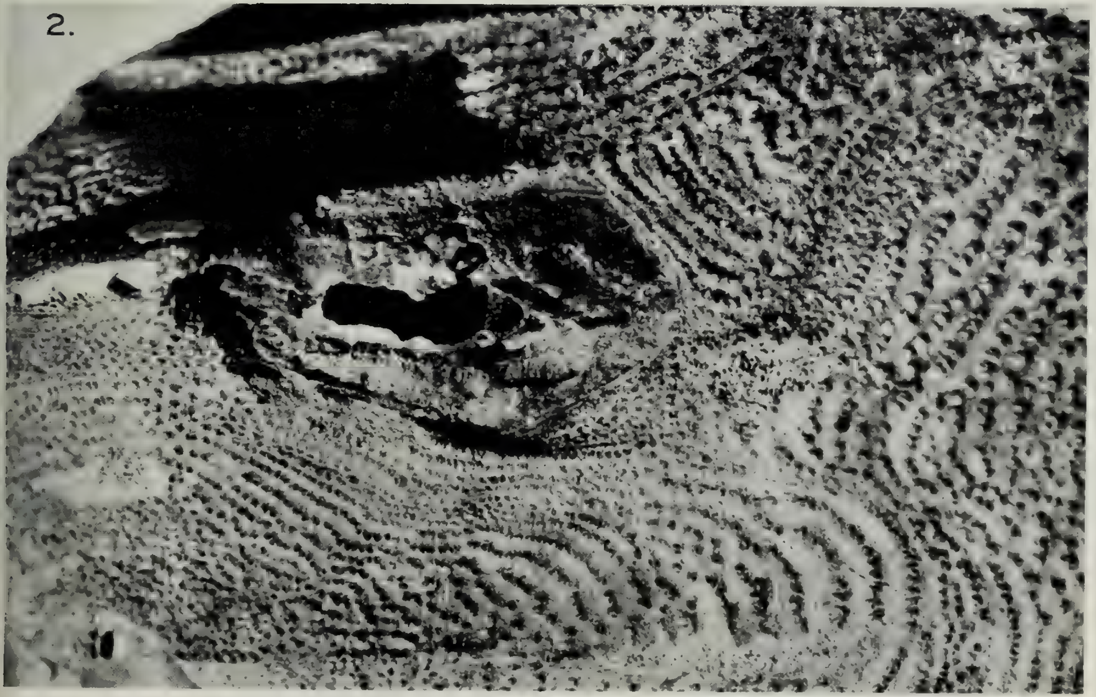


WILLIAMSASPIS BEDFORDI

PLATE 30

Buchanosteus murrumbidgeensis sp. nov.

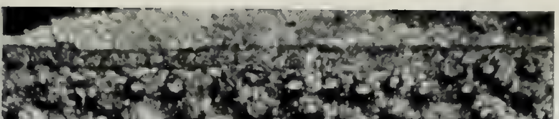
Fig. 1. Diagonal slice of skull. The holotype, P.27071, × 1½. (For explanation see Text-figs. 20, 21.)

Fig. 2. Unworn ornamentation of same, × 10.

Fig. 3. Portion of skull-roof of same, showing outer 'skin' with large tubercles covering underlying surface with smaller tubercles, the latter exposed in lower part, × 10.

Fig. 4. Worn ornamentation of small median dorsal plate, showing anterior margin. P.27072, × 10.

4.



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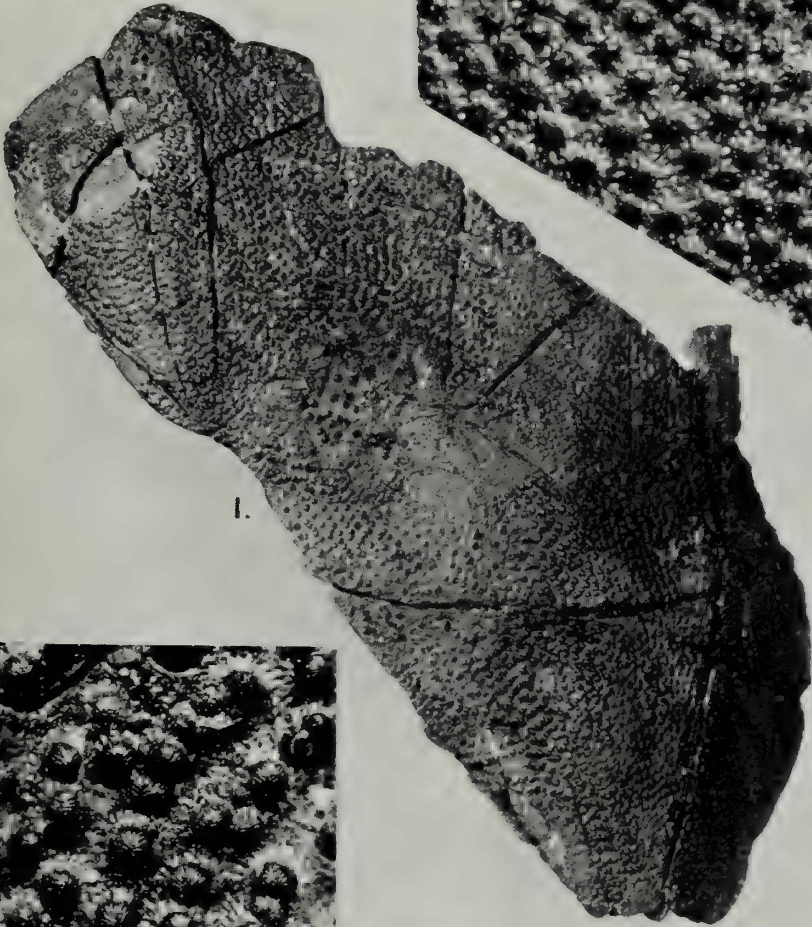

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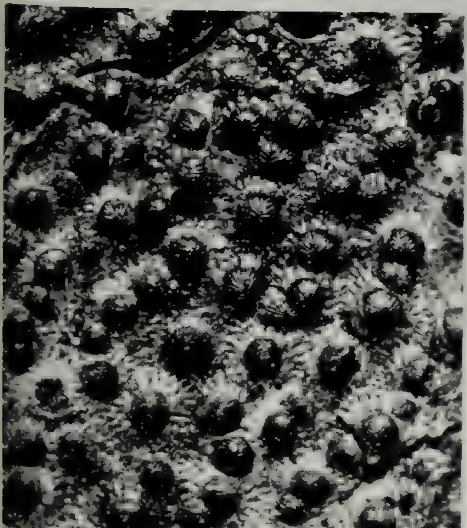

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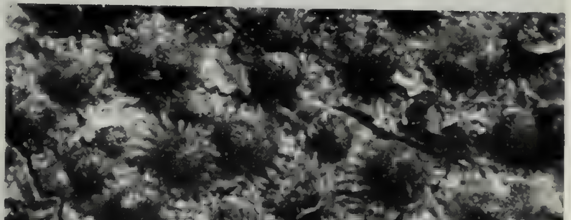


BUCHANOSTEUS MURRUMBIDGEENSIS

PLATE 31

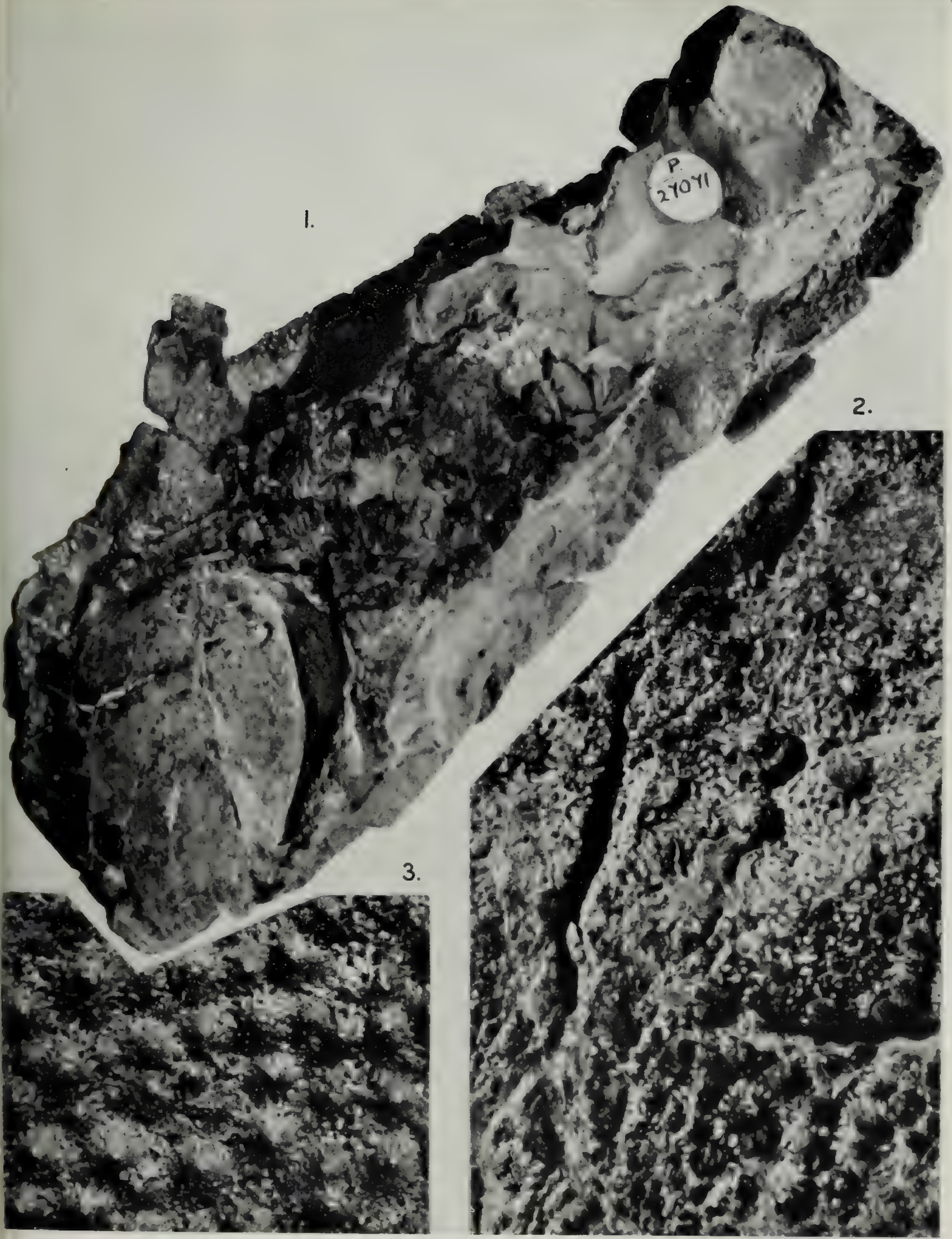
Buchanosteus murrumbidgeensis sp. nov.

Fig. 1. Undersurface of holotype lit from below. P.27071, × 2 approx. (For explanation see Text-fig. 22.)

Fig. 2. Part of dorsal surface of same showing large tubercles developed in damaged area (Sc. 3 in Text-fig. 20), normal ornamentation at bottom, × 10.

Taemasosteus novaustrocambricus gen. et sp. nov.

Fig. 3. Ornamentation of holotype. P.27070, × 10.



BUCHANOSTEUS and *TAEMASOSTEUS*

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PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY

21 OCT 1952

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GEOLOGY Vol. 1 No. 10
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(*University of Bristol*)

Pp. 305–324; *Pls.* 32, 33

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Issued October 1952 *Price Six Shillings*

CYCLOPYGID TRILOBITES FROM GIRVAN AND A NOTE ON *BOHEMILLA*

By W. F. WHITTARD

(UNIVERSITY OF BRISTOL)

SYNOPSIS

Two new genera and two new species belonging to the Cyclopygidae are described. The genus *Bohemilla* is here excluded from the Trilobita on account of certain exoskeletal details.

Mr. Ronald Tripp in re-examining the trilobite fauna from the Whitehouse Beds of Girvan, Ayrshire, as represented in the Gray Collection now in the British Museum, recognized several cranidia (attributed in manuscript by Reed to '? *Bohemilla*') as possibly belonging to *Phylacops*. He arranged for these specimens to be forwarded to me for study and, meanwhile, Mr. R. Baker was successful in finding in the unexamined material of the Gray Collection not only many better preserved specimens but also another new cyclopygid genus collected on the foreshore at Shalloch Mill.

Bohemilla is an exceptional and challenging fossil which is detached taxonomically from the cyclopygids, but a study of its morphology was clearly necessary since some workers had detected similarities between these arthropods.

Few monographs on fossils are written nowadays without help from other palaeontologists, and this short paper is no exception. Mr. R. Tripp was instrumental in directing my attention to some of the Girvan material I have described; Mr. R. Baker, Mr. A. G. Brighton, and Dr. J. C. Harper provided me with the opportunities for examining specimens in their charge; Professor H. B. Whittington and Dr. F. Prantl rendered valuable assistance by sending me photographs of type-specimens; Dr. C. J. Stubblefield and Dr. H. E. Hinton have discussed the structure and affinities of some of the fossils; Dr. Stanley Smith has derived the new generic names proposed in the text; and Mr. E. W. Seavill has prepared the photographs of the figured specimens from Britain.

The following abbreviations denote the museums in which the specimens are housed: BM: British Museum (Natural History); GSM: Geological Survey and Museum; MCZ: Museum of Comparative Zoology, Harvard; NM: Narodni Museum, Prague.

Family CYCLOPYGIDAE Raymond 1925

More than seventy years ago Nicholson & Etheridge (1880: 287) realized that the species of *Cyclopyge* known to them from Girvan could readily be separated into three distinctive groups, and they prophesied that in due course each would be accorded generic rank. *Cyclopyge* has been retained for the species comprising one of these groups, genotype *Cyclopyge rediviva* (Barrande, 1846: 34), wherein the large faceted eyes are developed as separate structures. In *Symphysops*, genotype *Symphysops armatus* (Barrande) (Raymond, 1925: 64), and *Phylacops*, genotype *Phylacops* *vigilans* (Cooper & Kindle, 1936: 366), the eyes are united anteriorly into a single element, but *Symphysops* is distinguished by the glabella being prolonged into a frontal spine. Two new genera, *Psilacella* and *Ellipsotaphrus*, are now added to the family.

Genus ***PSILACELLA***[1] nov.

Diagnosis. Glabella occupies most of the cranidium, carries three pronounced furrows; occipital ring absent. Fixed cheeks narrow and exceedingly small; axial furrow weak and continues as the preglabellar furrow. Facial sutures, probably confluent to form semi-elliptical outline, cut the posterior border close to the axial furrow; traced anteriorly they delimit, as far as the notch in their outline opposite the second glabellar furrow, the narrow and parallel-sided fixed cheeks, beyond which they form the edge of the brim passing round the outside of the preglabellar furrow. Multifaceted eyes assumed to unite anteriorly to form a single visual organ. Free cheeks unknown. Thorax unknown.

Pygidium sub-semicircular in shape; axis half pygidial length, carries five axial rings; three pairs of pleurae present and pleural lobes smooth posterolaterally.

Type species. *Psilacella trirugata* sp. nov.

Horizon and localities. Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay and Shalloch Mill, Girvan, Ayrshire.

Psilacella trirugata sp. nov.

(PLATE 32, FIGS. 1–5)

Diagnosis. As for genus.

Description. The new species is represented by three cranidia, two faceted eyes, and one pygidium, at one time all preserved on the same slab of mudstone where they were associated with a pygidium of the rare *Cyclopyge bumasti* Reed (BM: In. 44010, In. 44098–44100). The two isolated eyes may conceivably belong to the latter species, but one of the specimens shows the left eye extending sufficiently near to the mid-line as to suggest that the paired eyes approached close to one another around the front of the cephalon; assuming the correctness of this statement, this eye could not belong to *Cyclopyge bumasti*, and it is attributed to *Psilacella* which is the only other associated cyclopygid. One further cranidium, from Whitehouse Bay, is available (BM: In. 37090).

The cranidium of the holotype (BM: In. 44010) is strongly convex, 5·5 mm. in breadth and length, and ornamented with a delicate granulation which may be due more to peculiarities of preservation than to the structure of the exoskeleton. There is no occipital ring, apparently the posterior border furrow is absent and the fixed cheeks are minute; consequently the glabella constitutes most of the cranidium. None of the three pairs of furrows extends across the glabella and the space between each pair increases, the interval being about one-quarter of the glabellar breadth posteriorly and about one-third in the anterior pair. The second and posterior pairs of furrows run subparallel to the posterior border, but the anterior furrows pass obliquely forwards and inwards, and externally converge towards the second furrows. A narrow and gently concave fixed cheek, separated from the glabella by a feeble axial furrow, reaches from the posterior margin as far forward as the second glabellar furrow where there is a slight notch in the outline of the cranidium. Beyond this notch, which may mark the position of the hinder end of the faceted eye, the axial furrow continues as the preglabellar furrow and is attended externally by an exceedingly narrow flat brim.

---

[1] Ψιλάξ, one who is bald.

The lateral and front margins of the cranidium are well preserved not only in the holotype but also in one of the paratypes; thus the course of the facial suture can be determined. The suture commences at the posterior margin about 0·3 mm. outside the axial furrow, passes straight forwards, and delimits a fixed cheek which is so small as to be almost non-existent, forms a slight notch opposite the second glabellar furrow, thence runs outside the brim bordering the preglabellar furrow and is confluent with the facial suture of the opposite side; the facial sutures are interpreted as a single structure for which there is no obvious indication of a dual origin. The eye is provided with numerous facets of the normal cyclopygid pattern. One specimen (BM: In. 44100) is exceedingly difficult to interpret, but it is thought to represent the ventro-lateral aspect of a left eye squashed against the under surface of the cranidium; the outer margin of the specimen is a broken edge leading inwards to a narrow area, with terraced lines, which is prolonged into what simulates a spine but is probably nothing more than a trick of preservation. The inner margin of the eye is sigmoidal in form where it abuts against a concave surface, possibly to be identified as the rostral plate; the faceted region decreases in area when traced inwards and in front of this plate, and the general appearance suggests the eyes might be fused into a single visual organ.

The thorax is unknown.

The pygidium is almost twice as broad as long, and smoothly rounded in outline. The axis, which is slightly less than half the pygidial breadth measured along the anterior border, has the shape of a broad-based, inverted, stumpy triangle reaching posteriorly just beyond the mid-pygidial length, is well defined by axial furrows, and carries five clearly differentiated axial rings. Three pairs of pleurae alone can be detected, the postero-lateral portions of the pleural lobes being smooth; there is no postaxial ridge. The inclination of the border appears to change from vertical, posteriorly, to nearly horizontal, anteriorly, and it terminates behind the anterior pleurae which extend to the margin; a marginal furrow is present. The antero-lateral corners are sharply angular in outline, and here triangular facets are delimited by a deep furrow which is an extension of the furrow behind the articulatory half-ring.

Horizon and localities. Ordovician, Upper Whitehouse Beds, Ashgill Series: exposed on the foreshore at Whitehouse Bay and near Shalloch Mill, Girvan, Ayrshire.

Holotype. BM: In. 44010.

Other Specimens. BM: In. 37090, In. 44098–44100.

Discussion. The three paired glabellar furrows readily separate the new genus from *Phylacops vigilans* of the Whitehead Formation of Upper Ordovician (? Richmondian) age of Percé, Quebec (Cooper & Kindle, 1936: 367, pl. 52, figs., 36, 39, 41–51), and from *P. mirabilis* of the Portraine Limestone of Ashgill age of co. Dublin, Éire (Salter, 1853, pl. 10, figs. 1–7),[1] because these species are distinguished by one pair of lateral furrows. The Upper Tirnaskea Beds of Ashgill age, Zone of *Dicellograptus anceps*, of Pomeroy, Éire, contain cyclopygids which were first recorded as *Aeglina rediviva* (Fearnsides & others, 1907: 123, pl. 8, figs. 14–16). The fauna has recently been re-examined and one of the cyclopygids (Sedgwick Museum A. 16373) has been identified by Reed (in the press) as *P.* cf. *vigilans*. This specimen differs from *Psilacella trirugata* in the segmentation of the glabella and in the proportions of the pygidium and its axis.

The need for the new generic name of *Psilacella* was not determined until comparisons were made with the known species of *Phylacops* and also with certain trilobites from Bohemia; the latter appear to be most fittingly placed in *Phylacops* and this genus assumes a greater geographical distribution than was previously known. In their diagnosis for *Phylacops* Cooper & Kindle (1936: 366) mention that the eyes meet in front of the glabella, and elsewhere quote Nicholson & Etheridge (1880: 287) who, referring to *Cyclopyge mirabilis*, state that the eyes are 'united in front of the head to form one large optical organ'. Cooper & Kindle include *C. mirabilis* in *Phylacops*; in the photographs of the lectotype reproduced on Pl. 32, figs. 6–8, the binary origin of the eye is clearly shown in anterior view, where a shallow median groove, which is straddled by the facets, separates it into halves.

Klouček gave the briefest of descriptions, without illustrations, of two varieties of '*Aeglina*' wherein the eyes approach one another so closely, anteriorly, that they are separated by no more than a narrow band devoid of facets. One of these varieties recorded by Klouček (1919: 243, NM: CD 518) as *Aeglina speciosa* var. *synophthalma* was renamed for nomenclatorial reasons by Richter (1937: 301) as *Cyclopyge speciosa* var. *kloučeki*. This variety is so obviously different from *C. speciosa* (Barrande) that it should be given specific rank. The large size of the eyes and their extension around the glabellar front preclude the retention in *Cyclopyge*, and there appears to be no sound argument against including the species in *Phylacops* unless it be the presence of an unfaceted narrow strip separating the eyes (Pl. 32, fig. 9). For the present, therefore, *C. kloučeki* from the Svata Dobrotiva Shales of Malé Přilepy, near Beroun, central Bohemia, is placed in *Phylacops*. The shales are probably of Llandeilo age and correspond to the $d_{\gamma 2}$ horizon. The notation adopted here was suggested by Kettner & Kodym (1919)[2] and has been employed by most subsequent authors (Heritsch, 1928: 331; Kettner & Bouček, 1936, table IV). There have been several modifications, attended by some confusion, of the original notation proposed by Barrande, who used $Dd_{1\gamma}$ for the Osek and Kváň Beds and these include the well-known deposits of Šárka and Svata Dobrotiva. Klouček (1909), on the evidence of trilobites, subdivided the $d_{1\gamma}$ beds into $d_{1\gamma a}$ and $d_{1\gamma b}$, and these Kettner and Kodym relettered $d_{\gamma 1}$ and $d_{\gamma 2}$. The Šárka Beds ($d_{\gamma 1}$) are to be correlated with the zones of *Didymograptus bifidus* and *D. murchisoni* of Britain, and Bouček (1926: 542) suggests that the topmost horizon which yields *D. murchisoni* var. *clavulus* may even range into the Llandeilo (Zone of *Glyptograptus teretiusculus*).[1] The stratigraphically higher Svata Dobrotiva Beds ($d_{\gamma 2}$) accordingly are tentatively correlated with the Llandeilo Series, not because they yield graptolites of correlation value, but because they are succeeded by the Drabov Quartzite (d_{δ} beds), and these are followed by the Zahořany Beds (d_{ϵ}) which have produced graptolitic evidence for the presence of the Zones of *Dicranograptus clingani* and *Pleurograptus linearis* (Heritsch, 1928: 332; Bouček, 1928: 394).

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[1] *P. mirabilis* is usually attributed to Forbes; it was, however, first described by Salter who used Forbes's manuscript name.

[2] Reference is unverified as no copy of this publication has been traced.

Klouček (1919: 239, NM: CD 520) also records *Aeglina prisca* var. *synophthalma* from the Llanvirn Beds of Šárka ($d_{\gamma 1}$) and his short description of the eyes agrees almost word for word with that given by him for *P. kloučeki* (Richter). If the latter species is properly placed in *Phylacops* then the Llanvirnian form should be raised to specific level, because it is not a variety of *Cyclopyge prisca* (Barrande); it is here recorded as *Phylacops synophthalmus* (Klouček). The inclusion of the two Bohemian species in *Phylacops* gives the genus a larger stratigraphical range from Llanvirn to Ashgill and a wider geographical distribution than it was formerly thought to possess.

Genus ***ELLIPSOTAPHRUS***[2] nov.

Diagnosis. Cephalon subquadrate with rounded anterior outline; axial furrows diverge slightly from posterior border, thence sweep inwards meeting at mid-line in extremely obtuse angle: two glabellar furrows, the posterior entire and the anterior discontinuous and paired: occipital furrow[3] entire, merges into axial furrows to form with them and with the preglabellar furrow a ring-shaped groove: occipital ring strong and tumid. Fixed cheeks small, narrow, reach back to posterior border without pleuroccipital furrow, extend forwards for about one-third total cephalic length where they are confluent with a narrow brim running round the front of the glabella. The facial suture cuts the posterior margin 1 mm. outside the axial furrow, swings for a short distance slightly inwards and then markedly outwards nearly as far as the level of the second glabellar furrow, beyond which it curves inwards to meet the suture on the opposite side in an obtuse angle. Eyes coarsely multifaceted, fused into single element with no anterior median groove marking the line of fusion, concavo-convex in dorsal view, semicircular in outline on convex side.

Thorax incompletely known: axis broad, number of axial rings unknown but not less than four or five: pleurae short, bluntly terminated, each carries a pleural furrow.

Pygidium is known only in a crushed and downturned condition. Unfortunately the details cannot satisfactorily be determined, but the pygidium is apparently short relative to breadth, one pronounced ring can be detected on an axis which is about one-fifth the pygidial breadth, the anterior pleural border is tumid and succeeded posteriorly by a deep furrow, and there is one furrow on each pleural lobe.

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[1] Hede (1951: 54 and Table 5 facing p. 70) correlates the zone of *Didymograptus clavulus* of the Upper Didymograptus Shales of Sweden with the upper part of the Llanvirn.

[2] ἔλλειψις, ellipse, and τάφρος, ditch, allude to the characteristic form of the composite furrow surrounding the glabella.

[3] The interpretation of the posterior portion of the cephalic axis is difficult; either an occipital ring is present in the genotype, in which case the pleuroccipital furrow is absent on the fixed cheek, or the occipital ring is absent and the glabella extends to the posterior border. The former reading of the structure is followed here because what is probably a pleuroccipital furrow is found in *E. pumilio* and *E. infaustus* which otherwise closely resemble *E. monophthalmus*.

Type species. Ellipsotaphrus monophthalmus (Klouček).

Horizon and localities. The Svata Dobrotiva Shales probably of Llandeilo age $(\mathrm{d}_{\gamma 2})$[1] exposed in the brickyard in Prague XIX—Šárka (Vokovice), Bohemia (genoholotype); *Didymograptus bifidus* beds: Shropshire (Hope Shales), and near Llanfallteg railway station, Pembrokeshire.

Discussion. The diagnosis has been constructed from photographs of the holotype of *E. monophthalmus* from Bohemia (NM: CD 513; Pl. 32, figs. 10, 11), from Klouček's restoration of the cephalon (1919: pl. 1, figs., 4–6, reproduced here Pl. 32, figs. 12–14) and from several specimens collected from the *Didymograptus bifidus* beds of west Shropshire (Hope Shales) and of Pembrokeshire which show the indifferently preserved thorax associated with the cranidium (Whittard, 1940: 137, pl. 6, figs. 1–3); one specimen from Shropshire and another from Pembrokeshire are refigured for comparison with the genoholotype from Bohemia (Pl. 32, figs. 15, 16).

In 1940 I included *E. monophthalmus* in the then recently described *Phylacops* because, unlike any other cyclopygid genus, the paired eyes are completely fused into a single organ, but it is now realized that differences in the morphology of the glabella are sufficiently pronounced to be of generic, rather than specific, importance; for this reason the new genus *Ellipsotaphrus* has been named for the reception of *E. monophthalmus* and of two other, but stratigraphically younger, Ordovician species which appear to be closely related.

Ellipsotaphrus pumilio sp. nov.

(PLATE 33, FIGS. 1–3)

Diagnosis. Elliptical glabella possesses two furrows of which the anterior one is discontinuous; occipital ring not defined laterally by axial furrows; pleuroccipital furrows present but short. The combined facial sutures are semi-elliptical in shape; eyes assumed to be merged into a single organ.

Description. The cranidium varies in size, the smallest measuring 2·3 mm. long and 3 mm. broad, and the largest 3·8 mm. by 4·8 mm. The cranidium has generally been distorted during preservation, but in a few compressed specimens the glabella is surrounded by a composite furrow, ellipsoidal in shape, which immediately recalls the ring-shaped groove of *E. monophthalmus*. Like that species the glabella exhibits two furrows; the posterior one is complete and transverse, and the anterior is discontinuous over the mid-third of the glabellar breadth. The preglabellar, axial, and occipital furrows are interpreted as a confluent, ring-shaped groove. The occipital ring is indicated by the posteriorly convex portion of the hinder cranidial margin, but it is not delimited laterally by the axial furrows which do not continue behind the occipital furrow. The postero-lateral area existing outside the axial furrow and the occipital ring is divided into two portions by a short, horizontal, pleuroccipital furrow which, losing depth as traced inwards from the external margin, vanishes before the inferred lateral edge of the occipital ring is reached; the anterior portion, of crescentic shape, is identified as the fixed cheek and is separated along the length of the short pleuroccipital furrow from the almost parallel-sided posterior border.[1] The anterior border of the fixed cheek is occasionally seen to be feebly notched just in front of the level of the posterior glabellar furrow, indicating possibly the position of the backward extension of the eyes. The outline of the cranidium is preserved in several individuals and this shows the trend of the facial sutures; in combination, these sutures have the general form of an inverted horseshoe. The eyes are assumed to be fused or conjoined, although in the thirty specimens studied no cyclopygid eye-pattern has been detected in contact with the cranidium, but neither has it been observed in the British specimens of *E. monophthalmus*. A narrow brim, commencing at the position of the paired anterior glabellar furrow, extends round the front of the glabella.

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[1] See page 310 for a note regarding the correlation of these deposits.

Horizon and locality. Ordovician, Upper Whitehouse Group, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire. *E. pumilio* is associated with a rich trilobite fauna including *Agnostus 'perrugatus'* Barrande, *Ampyx* (*Lonchodomas*) *portlocki* Barrande, *Cyclopyge rediviva* (Barrande), *Dionide lapworthi* Nicholson & Etheridge, *Lichapyge? problematica* Reed, *Symphysops subarmatus* (Reed), *Shumardia scotica* Reed, and *Bohemilla scotica* Reed.

Dr. J. C. Harper sent me the cyclopygids collected by him from co. Clare, where, as at Girvan, they are associated with *Bohemilla* (Stubblefield, 1939: 61), and from co. Louth, Éire, but nothing resembling *Ellipsotaphrus* was detected.

Holotype. BM: In. 41750.

Other Specimens. BM: In. 21691, In. 21696, In. 44001.

Discussion. The labels accompanying two specimens (BM: In. 21691 and In. 21696) state that they are syntypes of *Bohemilla scotica* as selected by Reed (1904: 53 and 1914: 22); he failed, however, to separate what is now described as *E. pumilio* from *Bohemilla* and these two syntypes definitely belong to the new species

E. pumilio is distinguished from *E. monophthalmus* by the absence of axial furrows at the sides of the occipital ring and by the development of the pleuroccipital furrows; otherwise there is little detail on which to separate them.

Ellipsotaphrus infaustus (Barrande)

(PLATE 33, FIGS. 4, 5)

1852 *Trilobites infaustus* Barrande, p. 915, pl. 34, fig. 45.
1919 *Trilobites infaustus* Barrande: Klouček, p. 243.
1940 *Phylacops infaustus* (Barrande) Whittard, p. 138.

The only known specimen (NM: CD 855), preserved as an external mould in a soft black shale, is a subquadrate cranidium 4 mm. long and 4·8 mm. in maximum breadth. The glabella conforms to the generic pattern, both in shape and segmentation, but the occipital and axial furrows meet at an obtuse angle instead of flowing into a continuous curve. The occipital ring is pronounced, longest in the mid-line where it is also markedly convex in posterior outline, but the photograph submitted by

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[1] The terminology used for the parts of the posterior region of the cranidium is open to criticism, as also is the case in *E. monophthalmus* and *E. infaustus*, but the morphological arrangement is anomalous and unlike any other trilobite known to me.

Dr. Prantl (Pl. 33, fig. 4) does not show the axial furrows extending to the back border of the crandium. The fixed cheek is triangular, and the base is defined by the pleuroccipital furrow; the apex projects to a position midway between the two glabellar furrows, from whence a narrow brim sweeps forwards and inwards around the glabellar front, meeting its fellow medially in an almost continuous curve, but, as in *E. monophthalmus*, there is a slight angularity here in the outline. The margin of the cranidium appears to be undamaged and may be assumed to indicate the course of the facial sutures which is similar to that of *E. pumilio*; the eye is unknown.

Horizon and locality. Barrande did not specify the horizon of the holotype more fully than Étage D, and the locality is given by him as near Trubin in the neighbourhood of Beroun, Bohemia. Dr. Prantl has written to say that the specimen was obtained from the Cernin Beds ($\mathrm{Dd}_{\epsilon 2a}$), which are to be correlated with the Caradoc Series according to Kettner & Bouček (1936, table IV).

Holotype. NM: CD 855.

Discussion. The many resemblances between *E. monophthalmus* and *E. infaustus* led me (1940: 138) to believe the species might be synonymous, particularly in view of the uncertainty whether the lobe-like structure in the postero-lateral corner of Barrande's figure was really a portion of the fossil. In a personal communication Dr. Prantl remarks that Barrande's figure is a faithful portrayal of the holotype; *E. infaustus* can thus be separated on the failure of the axial furrow to attain the posterior border and on the presence of the pleuroccipital furrow. *E. infaustus* is, however, even closer to *E. pumilio* which, apart from being much smaller, apparently differs only in the incomplete pleuroccipital furrow and in the extension of the fixed cheek farther inwards behind the glabella.

CYCLOPYGID PYGIDIA

More than twenty detached cyclopygid pygidia, which cannot confidently be matched with any described members of the family, are associated with the cranidia of *Ellipsotaphrus pumilio*. Ranging from 2 to 4·5 mm. in breadth, at least four different kinds are recognizable, including some which are larval stages, and, as on the same slab of rock two or three kinds may occur adjacent to a cranidium of *E. pumilio*, there is at the moment no means to determine without dubiety which pygidium belongs to this species. One is similar to *Cyclopyge rediviva* and another to *Symphysops subarmatus*, and these are the only cyclopygids described by Reed from the particular rocks yielding *E. pumilio*; the remaining two kinds of pygidia are larval stages but do not belong to the same species.

Pygidium A

(Plate 33, fig. 6)

The pygidium (BM: In. 42539) is 4·7 mm. broad and 3 mm. long, the margin is smoothly rounded, and the anterior border is raised and succeeded posteriorly by a transverse groove. The axis is strongly defined by axial furrows, is one-half the length and a little more than one-quarter the breadth of the pygidium, and carries four rings which are terminated posteriorly by a conically shaped area. Three pairs of pleurae are well defined, there being at least two additional pairs although these are but faintly indicated; pleural furrows are moderately impressed and apparently extend outwards to the incompletely preserved margin. The axial furrows are in continuation posteriorly with a median postaxial furrow.

The presence of pleural furrows and, so far as can be determined, the absence of a marginal furrow, superficially distinguish the pygidium from that of *Symphysops subarmatus* (Reed, 1914: 21, pl. 3, fig. 9); but pygidium *A* is much smaller than the type of *S. subarmatus* and these small differences may be attributed to changes accompanying growth.

Horizon and locality. Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

Pygidium B

(PLATE 33, FIG. 7)

The pygidium (BM: In. 21701) is 3 mm. broad and 2 mm. long, semi-elliptical in shape; there is no lateral marginal furrow, and the anterior border is convex and marked posteriorly by a transverse furrow. The axis, which is half the length and slightly in excess of quarter the breadth of the pygidium, shows two strong rings and a conical terminal piece; a minimum of two pairs of pleurae, without pleural furrows, are present and additional pairs are vaguely outlined.

The specimen recalls the pygidium of the complete individual of an immature *Cyclopyge rediviva* (Barrande) figured by Reed (1904, pl. 8, fig. 2); a comparison of Barrande's and Reed's illustrations throws doubt on the correctness of Reed's identification because of the disparity in the details of the pygidia, in the number of thoracic segments (which may be due to a meraspid condition), and in the illaenid-like cephalon.

Horizon and locality. Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

Pygidium C

(PLATE 33, FIGS. 8, 9)

A diminutive pygidium, which is as broad as long and measures 2 mm. along the anterior border, is parallel-sided and rounded posteriorly (BM: In. 44006); the anterior border is raised, separated posteriorly by a transverse furrow, and the edges corresponding to the front of the pleural lobes are deflected in comparison with the articulatory surface of the axis. The well defined axis is about two-thirds the length and a little less than one-third the breadth of the pygidium, and carries five pronounced rings; five ungrooved pleurae almost attain the margin. The postaxial surface is smooth and axe-head in shape.

The pygidium is preserved close alongside a cranidium of *Ellipsotaphrus pumilio* and the proportions are consistent with them being parts of the same animal; the cranidial breadth is no more than a third of the measurement taken from the largest known specimens of *E. pumilio*, and it may be a larval form.[1] The number of pleurae relative to the pygidial size is also indicative of a young stage and it is probably a 'transitory pygidium'.

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[1] If this interpretation is correct, the characteristic details of the more mature cranidium have already appeared.

A slightly larger specimen (BM: In. 44110; Pl. 33, fig. 9) measuring 2·5 mm. across the front is obviously closely similar to the pygidium already described, but there are now four axial rings and four pleurae on each side; a shallow marginal furrow delimits a marginal border.

Horizon and locality. Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

Pygidium D

(PLATE 33, FIG. 10)

This type of pygidium is broader than long, measurements for two examples being 2 mm. and 3 mm. broad with corresponding lengths of 1·7 mm. and 2·3 mm., but otherwise there is a similarity with the outline of pygidium *C* particularly in respect to the subparallel sides. The broadly based axis possesses nine rings in the smallest pygidium (BM: In. 44000) and eight in the largest (BM: In. 42548); both show five unfurrowed pleurae and probably there are one or two further pleurae, but these are ill defined. A narrow border and a faintly impressed border furrow are present.

The larval pygidium *D* recalls pygidium *A* which is attributed provisionally to *Symphysops subarmatus*.

Horizon and locality. Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

INCERTAE SEDIS

Family BOHEMILLIDAE Barrande 1872

Klouček recognized certain similarities between *Bohemilla* and *Ellipsotaphrus infaustus*, and Reed attributed many specimens in the Gray Collection to *Bohemilla*, although most of these are now known to belong to *E. pumilio*. All the specimens of *B. stupenda* studied by Barrande are in the Schary Collection of the Museum of Comparative Zoology, Harvard, and I am obliged to Professor Whittington for sending me stereoscopic photographs of each; Dr. Prantl has also forwarded a photograph of the specimen described by Klouček. I have failed to determine the taxonomical relationships of this unusual arthropod, but the genus has been reviewed and Barrande's interpretation of the morphological structure vindicated.

Genus ***BOHEMILLA*** Barrande 1872

Bohemilla stupenda Barrande

(PLATE 33, FIGS. 11, 12)

1872 *Bohemilla stupenda* Barrande, p. 137, pl. 14, figs. 30–31 *non* fig. 32.
1896 *Aeglina stupenda* (Barrande) Beecher, p. 360, figs. 1–3.
1897 *Aeglina stupenda* (Barrande): Holm, p. 457.
1907 *Bohemilla stupenda* Barrande: Zelizko, p. 218.
1918 *Bohemilla stupenda* Barrande: Novák & Perner, p. 51.

1919 *Bohemilla stupenda* Barrande: Klouček, p. 244, fig. 10.
1923 ? *Bohemilla stupenda* Barrande: Klouček, p. 9, text-fig.

In his description of this bizarre arthropod Barrande used the specimen (MCZ: 4404) here selected as the lectotype, because this is the only specimen showing the posterior portion of the exoskeleton. The head-shield is composed of a median segmented region, 12 mm. long and 11 mm. broad, and lateral spinose cheeks with large eyes. The posterior or fifth segment is unlike the remaining cephalic segments and closely resembles those of the thorax; there is a threefold longitudinal subdivision into a central portion, showing a median sharp ridge, and two lateral portions each of which carries a backwardly directed furrow; the fifth segment no more than vaguely suggests a comparison with the occipital ring, the posterior border, and the pleuroccipital furrow of trilobites. The fourth cephalic segment is characteristic in shape because, as the paired third furrow is traced inwards from the lateral margin, it swings forwards on a convex curve, turns posteriorly as the mid line is approached, and ends in a hook-like extremity; the chevron-shaped median area, believed by Barrande to have morphological significance, may be accidental in origin, but it possesses much better-defined boundaries in the external mould, where it appears to send forward a prolongation on to the third segment, and assumes a spatulate shape. The third segment is bounded in front by the complete second furrow and shows two ridge-like tubercles one on each side of the mid-line. The second segment possesses a similar pair of elongated tubercles which lie immediately in front of those of the third segment; a marked reduction in the glabellar breadth occurs at the second glabellar furrow.[1] The frontal lobe is semicircular in shape and is defined posteriorly by the paired and incomplete first furrow; several cracks in the surface indicate that the lobe has been pressed down upon a narrow brim which appears to pass round the front.

The eye and most of the free cheek have been crushed and displaced relative to the glabella. A narrow band-like area with a marginal furrow occurs on the left of the posterior three glabellar segments and appears to be in place, but at the level of the second glabellar furrow and behind the eye this area is fractured across and slightly displaced outwards; thence the cheek and its attendant marginal furrow can be followed forwards, until it swings outwards and backwards as a narrow convex spine ornamented by terraced lines. For the most part the free cheek is thus reduced to a spine, a condition which recalls that found in *Deiphon*, where, however, the spine is carried on the fixed cheek. The portion of the cheek immediately in front of the eye is cracked, but it does not appear to be much disarranged; the anterior margin trends almost at right angles to the cranidial axis. The imperfectly preserved, coarsely faceted, and large eye extends back to the level of the second glabellar furrow and the posterior outline, as indicated by the concentric arrangement of the facets, is complete; although damaged anteriorly the left eye reaches as far forwards as the glabellar front, but is not seen to attain connexion in the mid-line with the right eye, a little of the faceted surface of which is preserved on the external mould. The facial suture, if present, remains undetected.

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[1] Although a trilobite terminology is used for convenience in description, *Bohemilla* is now excluded from that group of arthropods (see p. 320).

Six free segments occur posterior to the cephalon, and, if the last is identified as the pygidium, the thorax comprises five segments, all of which exhibit the same general structure. Each is divided into three parts; the middle is about one-half of the total thoracic breadth, carries a median ridge, and is separated from the lobate lateral regions by oblique and posteriorly directed furrows of seemingly complicated shape. The sixth segment is incompletely preserved and possesses a similar structure; it may thus represent the last thoracic segment, in which case a minute bifid surface at the posterior tip of the specimen may be interpreted as a fragment of a pygidium of unknown shape.

Lectotype. Museum of Comparative Zoology 4404.

Horizon and locality. The lectotype is stated by Barrande as coming from the Dd_1 beds of St. Benigna, Bohemia; Klouček records the species only from the $D_{1\gamma b}$ beds, which under a recent notation have been relettered $D_{\gamma 2}$ and placed in the Llandeilo Series of the Ordovician (see p. 310).

Discussion. In addition to the lectotype there were three other specimens available to Barrande, and one of these he figured (1872: pl. 14, fig. 32; MCZ: 4405A); they are preserved in a flattened condition in dark shale and have assumed a variety of forms which suggest they do not belong to *B. stupenda*; alternatively, the differences separating them from that species, or even from the genus, are elusive and difficult to define. The three additional specimens provide material with which to compare *B. stupenda*, and the incomplete cranidium, identified as belonging to that species by Klouček and utilized by him to refute Beecher's statement that Barrande had misinterpreted the structure of the lectotype, is also available.

The glabella figured by Barrande (*vide supra* and Pl. 33, fig. 13) is different in shape from that of the lectotype, being more rounded anteriorly where it is less damaged by compression, but the reduction in glabellar breadth at the second furrow is absent. The number of glabellar segments, the tubercles on the second and third segments, and the median ridge on the last segment are the same, but the disposition of some of the glabellar furrows is not identical.

A more distorted and apparently broader specimen (MCZ: 4406; Pl. 33, fig. 14) has retained the posterior part of the lateral surface of the cheek and its furrow; the margin of the cheek sweeps forward in a manner consistent with that shown by the lectotype, but there is a definite reduction in glabellar breadth, followed by an expansion, immediately in front of the first furrow, while on the right side a palpebral lobe may face the second segment.

The third additional specimen is the worst preserved (MCZ: 4405B; Pl. 33, fig. 15); here the reduction and expansion in glabellar breadth referred to above are more noticeable, a palpebral lobe is suggested on the photograph, but the elongated tubercles on the glabellar segments cannot be detected.

The specimen used by Klouček is in relief (NM: CD 523; Pl. 33, fig. 16); it is a poorly preserved example of a mould of the under surface of a cranidium, and a ridge on the occipital ring and tubercles on the glabella are not visible; the glabellar furrows are slightly different in form from those of *Bohemilla*, the occipital ring is well defined, the glabella is constricted in front of the first furrow and then expands anteriorly; most important, a palpebral lobe arises at the side of the constriction of the glabella, curves backwards and outwards and then turns inwards to meet the axial furrow near the middle of the second segment; the extreme anterior position of the palpebral lobe is unusual, but there is little doubt that this specimen is a trilobite.

The three forms studied by Barrande (MCZ: 4405A, 4405B, 4406) and the specimen attributed by Klouček to *B. stupenda* are in all probability members of the same species, but there is no real certainty that they can be placed in *Bohemilla*. The resemblances to *Bohemilla* are obvious, and accordingly misleading, but the anterior portion of the glabella and the form of the glabellar furrows are different in detail, and to identify these four specimens with *B. stupenda* is unsafe, particularly in view of their fragmentary condition. *B. stupenda* would thus be definitely represented only by the lectotype.

The only other occurrence of *Bohemilla* in Bohemia is from the Llanvirn Shales ($d_{\gamma 1}$) of Šárka. Novák identified a glabella associated with two thoracic pleurae as *B.* cf. *stupenda*, which Klouček (1919: 240) recorded, but did not figure, as *B. stupenda* var. *praecedens*; this differs from *B. stupenda* in possessing a broader front to the glabella.

Stubblefield (1939: 61) recognized the presence of *Bohemilla* among an Ashgillian fauna from co. Clare, Éire (Baily, 1862: 10, text-fig. 1*b*); because of the occurrence of *Dicellograptus complanatus* these beds can possibly be equated with the upper part of the Whitehouse Beds of Girvan, Ayrshire (Harper, 1942: 276).

Mrs. Gray recorded *Bohemilla* from the Whitehouse Beds of Ashgillian age of Whitehouse Bay, Girvan (*in* Peach & Horne, 1899: 517, 688), and Reed described the 'cranidia' but did not assign a specific name (1904: 53, pl. 8, fig. 4). Another and better preserved specimen was later obtained by Mrs. Gray and named *B. scotica* by Reed, who observed that this new species differs from *B. stupenda* particularly in the granulated ornament, in the shape of certain segments, and in the form of the furrows of the glabella (Reed, 1914: 22, pl. 4, fig. 1). I have recently exposed a further specimen (BM: In. 36987) which also demonstrates these differences and *B. scotica* can be accepted as an additional species which is also stratigraphically younger than *B. stupenda*.

Two specimens from Jämtland in Sweden were assigned by Linnarsson with great uncertainty to *Bohemilla* (*?*) *denticulata* (1875: 495, pl. 22, figs. 4, 5). Holm (1897: 457) re-examined the material, of which no new examples in the meantime had been collected, and, because Beecher (1896: 360) had produced reasons against the use of *Bohemilla* and hence Bohemillidae, he was constrained to place Linnarsson's specimens into known trilobite genera. Holm interpreted one specimen, showing large faceted eyes and what appear in Linnarsson's figures to be spines, as the underside of the head of *Aeglina*, and the pygidium, which was inaccurately illustrated, as a telephid. Whether Holm's new designations are correct, or not, is immaterial to the present study, because the specimens, incomplete and unsatisfactory as they are, are certain not to be retained in *Bohemilla*.

When reviewing the families and genera of trilobites Beecher found that *Bohemilla* was the only genus 'which could not be readily interpreted in terms of known trilobite morphology' (1896: 360), and he argued that the spinose cheek with its furrow and doublure was a part of the pygidial border which had become displaced. Beecher drew a restoration of the lectotype, replaced the 'pygidium' (which in any case is too large for the individual), added to the thoracic segments a series of imaginary pleurae for which there is not a shred of evidence, and claimed that because two small faceted areas at each lateral margin of the fifth glabellar segment had been overlooked, the eyes in reality extended the whole length of the cephalon. A careful examination of the excellent stereoscopic photographs of the lectotype reveals no such faceted areas in those positions, while the concentric arrangement of the facets with the posterior border of the eye shows that that structure is undamaged posteriorly. Beecher was imbued with the idea that *Bohemilla* is a trilobite possessing morphological features which are foreign to the known anatomy of the group and he unjustifiably attempted to explain away the anomalies by converting the lectotype of *Bohemilla* into *Cyclopyge*. Holm (1897: 457), who did not have the opportunity of examining the types, supported Beecher, but the present study has only confirmed Barrande.

The assessment of *Bohemilla* as a trilobite must now be attempted. When describing *B. scotica*, Reed was forced to observe that this anomalous arthropod may in fact be an arachnid; and evidently Beecher felt that certain of the generic peculiarities were so abnormal that they had to be accounted for in one way or another, but mainly on the grounds of misleading and incomplete preservation, in order to retain the genus in the comity of trilobites. *Bohemilla*, however, finds no ready place among any known family and it is here excluded from the Trilobita by virtue of the following exoskeletal details: the anterior position of the spine of the so-called free cheek and its relation to the eye are atypical; the sudden reduction in glabellar breadth at the second furrow cannot be matched among trilobites and neither can the unusual trend of the third furrow; the paired tubercles on the second and third glabellar segments, the median chevron-shaped area on the third glabellar segment, and the median ridges on the fifth glabellar and on all the thoracic segments find no obvious parallel among trilobites; the absence of anything directly to be recognized as pleurae on the thoracic segments is a difference of fundamental importance. Having advanced reasons in favour of excluding *Bohemilla* from the Trilobita, a greater problem remains in finding a subdivision of the Arthropoda into which it can be accepted. Dr. H. E. Hinton, who kindly examined the photographs, said that he could perceive no diagnostic features which suggest comparison with any particular group of arthropods. The taxonomic position of *Bohemilla* thus remains unsolved, and it must rest for the moment as an example wherein the exoskeletal structures are, on the one hand, sufficient to exclude it from the Trilobita and, on the other hand, insufficient to provide that kind of evidence upon which the worker among modern arthropods relies in framing classifications.

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PLATE 32

Psilacella trirugata gen. et sp. nov.

The specimens are from the Ordovician, Upper Whitehouse Beds, Ashgill Series: Shalloch Mill, Girvan, Ayrshire.

Fig. 1. Dorsal view of cranidium, of which much of the exoskeleton is preserved, to show the glabella and its three paired furrows, and the reduced fixed cheeks. Holotype. ×3. (BM: In. 44010.)

Fig. 2. Internal mould of another specimen. ×3. (BM: In. 44098.)

Fig. 3. Side view of same specimen to show the externally convergent first and second glabellar furrows, the fixed cheek reduced to a narrow area, and the narrow brim which runs round the glabellar front. ×3.

Fig. 4. Ventral view of crushed left eye associated with what may be a portion of the rostral plate; the facets can be traced to the left and in front of the remnant of this plate. ×6. (BM: In. 44100.)

Fig. 5. Pygidium showing articular facets, stumpy segmented axis, and pleurae. ×3. (BM: In. 44099).

Phylacops mirabilis Forbes MS., Salter.

Figs. 6–8. Top, oblique side, and front views of the lectotype from the Ordovician, Portraine Limestone, Ashgill Series: co. Dublin. Note that the facets shown in Fig. 8 extend across the median groove and the eyes are united into a single organ. ×4. (GSM: 35571.)

Phylacops kloučeki (Richter)

Fig. 9. Front view to show the narrow smooth band which is left owing to the failure of the paired eyes to fuse anteriorly along the median line. Llandeilo Series ($D_{\gamma 2b}$ beds): Malé Přilepy, Bohemia. ×2. (NM: CD 518; photograph by National Museum, Prague.)

Ellipsotaphrus monophthalmus (Klouček)

Figs. 10, 11. Dorsal and oblique frontal view of distorted genoholotype to show glabellar furrows and fused eye. Llandeilo Series ($D_{\gamma 2b}$ beds): Vokovice, Bohemia. ×3. (NM: CD 513; photographs by National Museum, Prague.)

Figs. 12–14. Reproduction of Klouček's restoration of the cephalon (1919, pl. 1, figs. 4–6). ×3.

Fig. 15. Internal mould of a cranidium to show general morphology. Hope Shales (Zone of *D. bifidus*): Hope Dingle Stream, 92 yards south of Hope Villa, Shropshire. ×3. (GSM: RR 614.)

Fig. 16. Internal mould to show cranidium, displaced thoracic segments, and down-turned pygidium. *D. bifidus* beds: Cefn Farchen Farmyard, 7/8 mile south-east of Llanfallteg railway station, Pembrokeshire. ×3. (GSM: Pr 2033.)

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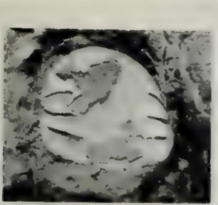
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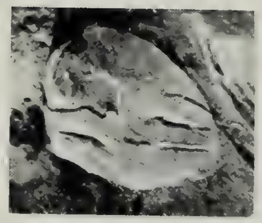
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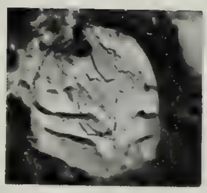
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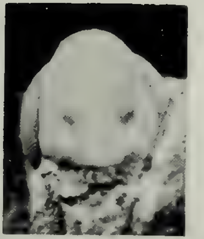
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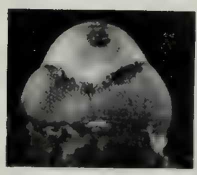
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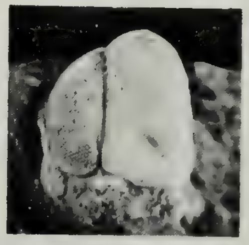
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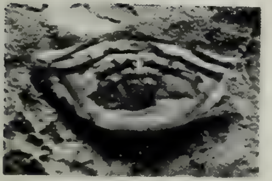
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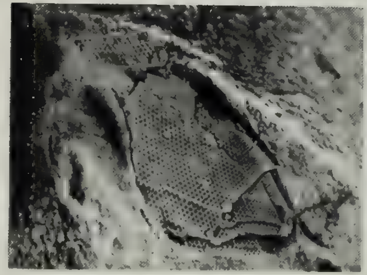
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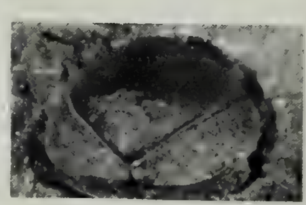
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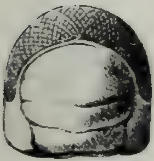
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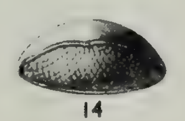
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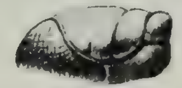
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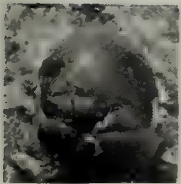
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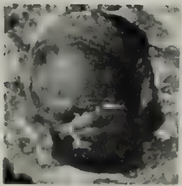
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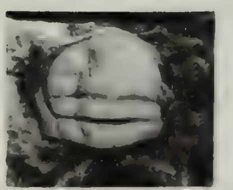
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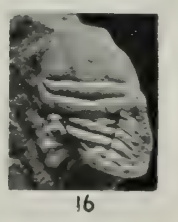
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PSILACELLA, PHYLACOPS, ELLIPSOTAPHRUS

PLATE 33

Ellipsotaphrus pumilio gen. et sp. nov.

The specimens are from the Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

Fig. 1. Internal mould of small individual to show glabellar furrows, occipital ring and short pleuroccipital furrow. Holotype. ×6. (BM: In. 41750.)

Fig. 2. Internal mould of larger individual showing general structure. ×6. (BM: In. 44001.)

Fig. 3. Internal mould. ×6. (BM: In. 21691.)

Ellipsotaphrus infaustus (Barrande)

Fig. 4. External mould of holotype showing occipital and pleuroccipital furrows in continuation with one another, and the fixed cheek. Caradoc Series, Cernin Beds ($Dd_{\epsilon 2a}$): Trubin, Bohemia. ×4. (NM: CD 855; photograph by National Museum, Prague.)

Fig. 5. Reproduction of Barrande's illustration of holotype (1852, pl. 34, fig. 45). ×4.

Cyclopygid pygidia

The specimens are from the Ordovician, Upper Whitehouse Beds, Ashgill Series: Whitehouse Bay, Girvan, Ayrshire.

Fig. 6. Pygidium, type *A*, which compares with *Symphysops subarmatus*. ×6. (BM: In. 42539.)

Fig. 7. Pygidium, type *B*, which compares with the specimen figured by Reed as *Cyclopyge rediviva* (1904, pl. 8, fig. 2). ×6. (BM: In. 21701.)

Fig. 8. Pygidium, type *C*, showing five axial rings and five pairs of pleurae, and axehead-shaped posterior area; this is probably a transitory pygidium. ×6. (BM: In. 44006.)

Fig. 9. Pygidium, type *C*, slightly larger than, but comparable with, the previous pygidium and showing four pronounced axial rings and four pairs of pleurae. ×6. (BM: In. 44110.)

Fig. 10. Pygidium, type *D*, showing seven or eight axial rings and five pairs of pleurae. ×6. (BM: In. 42548.)

Bohemilla stupenda Barrande

Fig. 11. Internal mould of lectotype to show general structure. Llandeilo Series (Dd_1 beds, now relettered $D_{\gamma 2}$): St. Benigna, Bohemia. ×1·5. (Schary Collection, MCZ: 4404; photograph by Prof. H. B. Whittington.)

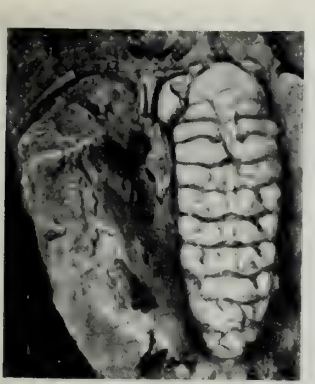
Fig. 12. External mould of same individual. ×1·5. (Photograph by Prof. H. B. Whittington.)

Gen. indet.

Fig. 13. Internal mould of compressed cranidium, figured by Barrande (1872, pl. 14, fig. 32). ×3. Llandeilo Series (Dd_1 beds, relettered $D_{\gamma 2}$): St. Benigna, Bohemia. (Schary Collection, MCZ: 4405A; photograph by Prof. H. B. Whittington.)

Figs. 14, 15. Internal moulds studied, but unfigured, by Barrande. There is considerable doubt whether these incomplete and distorted cranidia (figs. 13–15) belong to *Bohemilla*; they show most similarity to the original of Fig. 16. Same locality and horizon. ×3. (fig. 14, Schary Collection, MCZ: 4406; fig. 15, MCZ: 4405B; photographs by Prof. H. B. Whittington.)

Fig. 16. The original specimen attributed by Klouček (1923) to *Bohemilla stupenda*; its nearest parallel is Fig. 14 and for the moment should be excluded from *Bohemilla*. Note the palpebral lobe on the right side. St. Benigna Beds ($Dd_{\gamma 2}$): Malé Přilepy, Bohemia. ×2. (NM: CD 523; photograph by National Museum, Prague.)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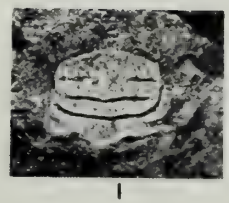
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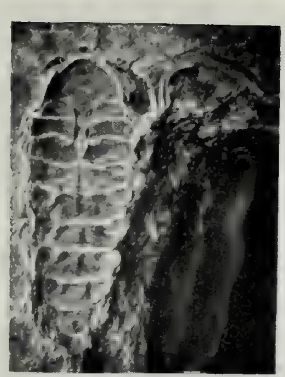
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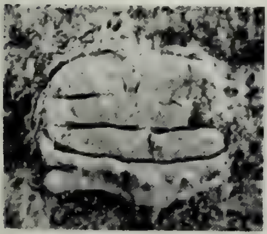
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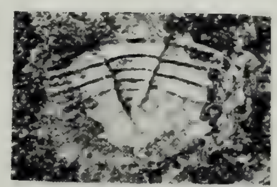
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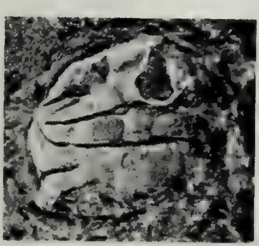
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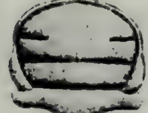
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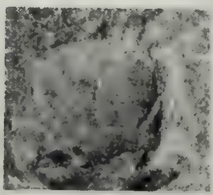
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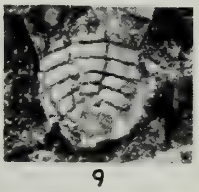
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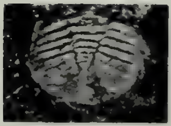
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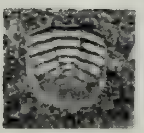
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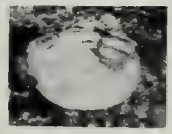
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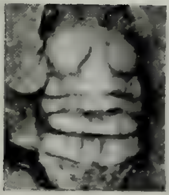
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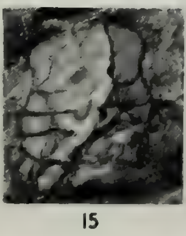
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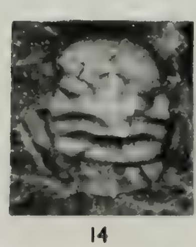
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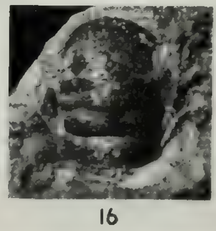
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ELLIPSOTAPHRUS, BOHEMILLA

BRITISH MUSEUM NATURAL HISTORY
PRESENTED
21 OCT 1952

NATURAL HISTORY

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BRITISH MUSEUM NATURAL HISTORY
PRESENTED
7 JUL 1953

PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY